

1 **Towards a phylogenetic taxonomy of sturgeons (*Acipenseriformes: Acipenseridae*)**

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8

9 **Abstract.**

10 *Acipenseriformes*, comprising sturgeons and paddlefishes, is one of the three ancient and  
11 species-poor living lineages of non-teleost *Actinopterygii*. Here, we use DNA sequence  
12 and morphological data to investigate the phylogenetic relationships of sturgeons and  
13 produce a phylogenetic basis for the taxonomy of *Acipenseridae*. We resolve five major  
14 clades within sturgeons. As in previous studies, species of *Scaphirhynchus* and  
15 *Pseudoscaphirhynchus* each resolve as monophyletic groups, whereas *Huso* and  
16 *Acipenser* are paraphyletic. To render all acipenserid genera monophyletic, we confine  
17 *Acipenser* to *A. sturio* Linnaeus 1758, *A. oxyrinchus* Mitchill 1815, and *A. desotoi*  
18 Vladykov 1955, and resurrect the genus name *Sinosturio* Jaekel 1929 for a well-  
19 supported clade consisting of *Sinosturio dabryanus* (Duméril 1869), *S. sinensis* (Gray  
20 1835), *S. transmontanus* (Richardson 1836), *S. schrenckii* (Brandt 1869), *S. medirostris*  
21 (Ayres 1854), *S. mikadoi* (Hilgendorf 1892), and *S. dauricus* (Georgi 1775). Phylogenies  
22 that we infer using concatenated nuclear genes and concatenated nuclear and  
23 mitochondrial DNA sequences resolve *Huso huso* (Linnaeus 1758) and ten species  
24 traditionally classified as *Acipenser* as a monophyletic group. We suggest applying the  
25 genus name *Huso* to this lineage. Our analyses provide a robust framework for a  
26 phylogenetic taxonomy of sturgeons and a foundation for future studies of the  
27 relationships and ages of acipenserid clades.

28 **Keywords:** *PhyloCode*; *Acipenseriformes*; *Acipenseridae*; sturgeon; taxonomy;  
29 systematics; phylogenetics

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31

32 In the 21<sup>st</sup> century, molecular phylogenies have produced a broad consensus  
33 surrounding the evolutionary relationships of ray-finned fishes, the *Actinopterygii*  
34 (Dornburg and Near 2021). This emerging phylogeny has formed the basis of taxonomies  
35 of ray-finned fishes using both traditional ranked (i.e., Linnaean) and rank-free (i.e.,  
36 *PhyloCode*) strategies (Betancur-R et al. 2017; Dornburg and Near 2021; Near and  
37 Thacker 2024). A phylogeny-based rank-free taxonomy of *Actinopterygii* is enabled by a  
38 set of phylogenetic analyses that consistently resolve a fairly congruent ray-finned fish  
39 tree of life (Near et al. 2012; Miya and Nishida 2015; Hughes et al. 2018; Dornburg and  
40 Near 2021; Near and Thacker 2024). Although the relationships among the major  
41 lineages of *Actinopterygii* and *Teleostei* are largely resolved, the phylogenies of a few  
42 deeply divergent lineages of ray-finned fishes remain unclear (Dornburg and Near 2021;  
43 Near and Thacker 2024).

44 One of the most ancient clades of ray-finned fishes is *Acipenseriformes* (sturgeons  
45 and paddlefishes), which, along with *Polypteridae* (bichirs and Reedfish) and *Holostei*  
46 (gars and bowfins), form a grade leading to the hyper-diverse *Teleostei* (Near et al. 2012;  
47 Betancur-R et al. 2017; Hughes et al. 2018; Dornburg and Near 2021; Near and Thacker  
48 2024). Sturgeons and paddlefishes are characterized by a mouth positioned ventrally, a  
49 developed rostrum composed of a high number of ossifications, a poorly ossified  
50 skeleton, and a heterocercal tail (Bemis et al. 1997; Hilton et al. 2011). The fossil record  
51 of *Acipenseriformes* stretches back to the early Mesozoic and includes representatives of  
52 both living clades known from complete skeletons (Grande and Bemis 1991; Bemis et al.  
53 1997; Bemis and Kynard 1997; Hilton et al. 2011; Sato et al. 2018; Murray et al. 2020;  
54 Hilton et al. 2021; Brownstein 2023; Hilton et al. 2023; Hilton and Grande 2023; Martill  
55 2023; Murray et al. 2023). The body plans of the 27 living species of sturgeons and the  
56 single surviving extant paddlefish *Polyodon spathula* closely resemble those of extinct  
57 forms dating to the Late Cretaceous (Grande and Bemis 1991; Hilton et al. 2011; Sato et  
58 al. 2018; Murray et al. 2020; Hilton et al. 2023; Hilton and Grande 2023; Murray et al.  
59 2023), and the conserved morphology and low molecular evolutionary rates of sturgeons  
60 and paddlefishes has led to them being labeled living fossils (Gardiner 1984; Grande and  
61 Bemis 1991; Bemis et al. 1997; Hilton et al. 2011; Brownstein et al. 2024).

62 The phylogeny of *Acipenseriformes* has been investigated using morphological  
63 characters (Grande and Bemis 1996; Mayden and Kuhajda 1996; Findeis 1997;  
64 Artyukhin 2006; Hilton and Forey 2009; Hilton et al. 2011) and DNA sequence data  
65 (Birstein and DeSalle 1998; Doukakis 2000; Birstein et al. 2002; Dillman et al. 2007;  
66 Peng et al. 2007; Krieger et al. 2008; Luo et al. 2019; Nedoluzhko et al. 2020; Shen et al.  
67 2020; Cheng et al. 2021). Yet, the systematics of the *Acipenseriformes*, particularly  
68 lineages within *Acipenseridae* (sturgeons), remains controversial. This is chiefly because  
69 both *Acipenser* Linnaeus 1758 and *Huso* Linnaeus 1758 are paraphyletic in phylogenies  
70 inferred from both morphological and molecular data (Birstein and DeSalle 1998;  
71 Birstein et al. 2002; Dillman et al. 2007; Peng et al. 2007; Krieger et al. 2008; Hilton et  
72 al. 2011; Luo et al. 2019; Shen et al. 2020; Shedko 2022; Dadkhah et al. 2023). Because  
73 of the massive sizes of acipenserid genomes, orthologous nuclear gene sets are difficult to  
74 assemble across sturgeon diversity; this has led to a reliance on mitochondrial DNA  
75 (mtDNA) for inferring the phylogeny of *Acipenseridae* (Ludwig et al. 2001; Du et al.  
76 2020). Together, these issues hamper the reconciliation of acipenserid taxonomy with the  
77 phylogeny of this clade.

78 Sturgeons rank among the most globally endangered vertebrate groups (White et  
79 al. 2023; [IUCN] International Union for Conservation of Nature 2024). The 20th century  
80 saw a rapid expansion of the global sturgeon fishery, driven by increasing demand for  
81 caviar and sturgeon meat (Bronzi et al. 2019). This expansion led to a severe decline in  
82 sustainable sturgeon populations worldwide (Raymakers and Hoover 2002; White et al.  
83 2023). The potential existence of cryptic species within already endangered sturgeon  
84 lineages (e.g., Birstein et al. 2005) highlights the critical need for a taxonomy that  
85 accurately reflects the phylogenetic relationships within this clade. Such a taxonomy is  
86 essential for conservation efforts and management strategies that effectively conserve  
87 both species diversity and unique evolutionary history (Gumbs et al. 2024).

88 Here, we use a combination of mtDNA, nuclear DNA, and morphological  
89 characters to assess the phylogenetic relationships of sturgeons and produce a revised  
90 rank-free classification of *Acipenseridae*. Our revision includes the resurrection of  
91 *Sinosturio* Jaekel in Weigelt (1929) for the genus group name of clade of species  
92 distributed primarily in Pacific regions of Asia and North America (Birstein et al. 2002;

93 Dillman et al. 2007; Peng et al. 2007; Krieger et al. 2008; Luo et al. 2019; Shen et al.  
94 2020; Shedko 2022) and the expansion of *Huso* to comprise a clade of sturgeons  
95 distributed in primarily the Atlantic, Siberian Sea, Black Sea, Caspian Sea, Adriatic Sea,  
96 and Aral Sea (Table 1).

97

## 98 **Materials and Methods**

99

100 **Molecular Sequence Dataset and Morphological Dataset Assembly.** The molecular  
101 datasets used in this study were constructed from NCBI and the morphological data is  
102 reanalyzed from scientific publications. Because the data we use is compiled from several  
103 studies from different research groups, DNA sequences representing individual species  
104 do not necessarily come from the same individual specimens. We compiled *cytochrome b*  
105 (*cytb*) sequence data from the mitochondrial genomes of every species of sturgeon and  
106 paddlefish. We combined these data with DNA sequences from the 30 nuclear genes  
107 (Luo et al. 2019). All molecular data used in this study were extracted from the NCBI  
108 database GenBank. NCBI accession numbers for each sequence are provided in Tables  
109 S1 and S2. Given that all the genes used in this study are protein coding and there were a  
110 limited number of insertions and deletions in the gene sequences among the sampled  
111 species, sequences of *cytb* and each of the nuclear genes were aligned manually by eye.  
112 We expanded a morphological dataset used in a previous phylogenetic analysis of  
113 *Acipenseriformes* (Hilton et al. 2011) to include the species †*Acipenser praeparatorum*  
114 Hilton and Grande 2023 from the Maastrichtian Hell Creek Formation (Hilton and  
115 Grande 2023). Several recently described extinct species of sturgeons were not included  
116 owing to the highly incomplete nature of known fossils (Murray et al. 2020; Hilton and  
117 Grande 2023; Murray et al. 2023).

118

119 **Maximum Likelihood Analyses.** We inferred the phylogenetic relationships of  
120 sturgeons using maximum likelihood analyses of the alignments of the *cytb* gene, the  
121 combined 30 nuclear genes, and a concatenated dataset of the *cytb* and 30 nuclear genes  
122 using IQ-TREE (Nguyen et al. 2015). In analyses of each dataset, we allowed for free-  
123 rate heterogeneity and assessed nodal support using 1000 ultrafast bootstraps

124 and 1000 replicates of the Shimodaira–Hasegawa approximate likelihood ratio (SH-r)  
125 test. We selected optimal models of nucleotide evolution using ModelFinder Plus  
126 (Nguyen et al. 2015; Kalyaanamoorthy et al. 2017).

127

128 **Bayesian Tip-Dating Analyses.** Using the modified morphological dataset of Hilton et  
129 al. (2011) and input ages from Shedko (2022), we conducted a Bayesian tip-dating  
130 analysis in BEAST 2.6.6 (Bouckaert et al. 2019) using the Fossilized Birth-Death Model  
131 (Gavryushkina et al. 2017). We partitioned the morphological characters by state count  
132 and used the Markov-variable model of discrete morphological character evolution  
133 (Lewis 2001). We used a relaxed log-normal clock model and set the origin prior to 254.1  
134 Ma, which is the lower boundary of the Wuchiapingian Stage of the Permian Period and  
135 approximates the oldest fossils attributable to total clade *Acipenseriformes* (Liu and Wei  
136 1988), assuming resolution of †*Saurichthyiformes* as the sister lineage of *Chondrostei*  
137 total group (Argyriou et al. 2022). We set the lower bound as the base of the Triassic,  
138 251.9 Ma, which approximates the median bound found for pan-acipenseriforms (Shedko  
139 2022), and the upper bound to 358.9 Ma, the Carboniferous-Devonian Boundary, which  
140 is the approximate upper bound for the split between *Acipenseriformes* and *Neopterygii*  
141 estimated in relaxed molecular clock analyses (Near et al. 2012; Hughes et al. 2018; Bi et  
142 al. 2021). We set the diversification rate parameter to 0.11, which is the number of living  
143 species in the dataset divided by the median origin time, and rho, the proportion of living  
144 species sampled, to 1.0. We constrained †*Chondrosteus acipenseroides* Egerton 1858 as  
145 the outgroup and performed two independent analyses using BEAST 2.6.6 with  $5.0 \times 10^7$   
146 generations augmented by a pre-burnin of  $1.0 \times 10^7$  generations. We checked ESS values  
147 and conversion of the posteriors using Tracer 1.7.1 (Rambaut et al. 2018). Posterior tree  
148 files were combined and summarized into a maximum clade credibility tree with median  
149 node heights using LogCombiner v. 2.6.7 and TreeAnnotator v. 2.6.6 (Bouckaert et al.  
150 2019).

151 For each of the six fossil calibrations we justify the phylogenetic placement,  
152 provide information on the stratigraphy, and give the age used in the fossil tip-dated  
153 relaxed clock analyses:

154

155 †*Chondrosteus acipenseroides* Egerton 1858

156 **Phylogenetic placement:** †*Chondrosteus acipenseroides* is placed as the sister to  
157 crown *Acipenseriformes* based on the results of previous phylogenetic analyses  
158 and results of Bayesian tip-dated phylogenetic analysis of morphological  
159 characters conducted in this study (Hilton and Forey 2009; Hilton et al. 2011;  
160 Shedko 2022).

161 **Stratigraphy:** Triassic-Jurassic of Dorset, England (Egerton 1858; Hilton and  
162 Forey 2009).

163 **Fossil tip age:** 201.3 Ma (Shedko 2022).

164

165 †*Peipiaosteus pani* Liu and Zhou 1965

166 **Phylogenetic placement:** †*Peipiaosteus pani* is the sister lineage of all other pan-  
167 polyodontids in *Acipenseriformes* in our Bayesian tip-dated phylogenetic analysis  
168 of morphological characters.

169 **Stratigraphy:** Yixian Formation, Liaoning, China; Barremian Stage of the Early  
170 Cretaceous (Liu and Zhou 1965; Jin 1999).

171 **Fossil tip age:** 125.0 Ma (Shedko 2022)

172

173 †*Protopsephurus liui* Lu 1994

174 **Phylogenetic placement:** †*Protopsephurus liui* is placed as the sister to  
175 *Polyodontidae* in *Acipenseriformes* based on previous phylogenetic analyses and  
176 the results of Bayesian tip-dated phylogenetic analysis of morphological  
177 characters conducted in this study (Grande et al. 2002; Hilton and Forey 2009;  
178 Hilton et al. 2011; Shedko 2022).

179 **Stratigraphy:** Yixian Formation, Liaoning, China; Barremian Stage of the Early  
180 Cretaceous (Lu 1994; Jin 1999; Grande et al. 2002).

181 **Fossil tip age:** 125.0 Ma (Shedko 2022).

182

183 †*Priscosturion longipinnis* (Grande and Hilton 2006)

184 **Phylogenetic placement:** †*Priscosturion longipinnis* is placed as the sister  
185 lineage of all other pan-acipenserids in *Acipenseriformes* based on the results of

186 Bayesian tip-dated phylogenetic analysis of morphological characters conducted  
 187 in this study, as well as previous phylogenetic analyses (Grande and Hilton 2006;  
 188 Hilton and Forey 2009; Hilton et al. 2011; Shedko 2022).

189 **Stratigraphy:** Judith River Formation, Alberta, Canada; early Campanian Stage  
 190 of the Late Cretaceous (Grande and Hilton 2006).

191 **Fossil tip age:** 79.6 Ma (Shedko 2022).

192

193 †*Anchiacipenser acanthaspis* Sato, Murray, Vernygora, and Currie 2018

194 **Node calibrated:** †*Anchiacipenser acanthaspis* is placed as the sister lineage of  
 195 *Acipenseridae* in *Acipenseriformes* based on the results of Bayesian tip-dated  
 196 phylogenetic analysis of morphological characters conducted in this study.

197 **Stratigraphy:** Dinosaur Park Formation, Alberta, Canada; late Campanian Stage  
 198 of the Late Cretaceous (Sato et al. 2018).

199 **Fossil tip age:** 75.5 Ma (Shedko 2022).

200

201 †*Acipenser praeparatorum* Hilton and Grande 2023

202 **Node calibrated:** †*Acipenser praeparatorum* is placed as the sister lineage of a  
 203 clade containing species of *Huso* and *Pseudoscaphirhynchus* in *Acipenseridae*  
 204 based on the results of Bayesian tip-dated phylogenetic analysis of morphological  
 205 characters conducted in this study.

206 **Stratigraphy:** Hell Creek Formation, North Dakota, USA; late Maastrichtian  
 207 Stage of the Late Cretaceous (Hilton and Grande 2023).

208 **Fossil tip age:** 66.0 Ma (Gale et al. 2020; Gradstein and Ogg 2020).

209

210 For the tip-dated Bayesian analysis of the concatenated molecular dataset, we  
 211 inserted the six fossils with ‘NNN’ strings and fixed their positions based on the tip-dated  
 212 Bayesian phylogeny generated using the morphological character matrix. We used the  
 213 Fossilized Birth-Death Model with the Lognormal Relaxed Clock prior, a JC69 model of  
 214 nucleotide evolution, and among-site rate variation with a gamma distribution. The origin  
 215 prior and its bounds were the same as in the analysis of the morphological character  
 216 matrix. We set the diversification rate parameter to 0.14, which is the number of species



217 sampled in the dataset divided by the origin prior. We set rho to 1.0 as all living species  
218 were sampled. As with the Bayesian analysis of the morphological dataset, we performed  
219 two independent analyses using BEAST 2.6.6 with  $5.0 \times 10^7$  generations augmented by a  
220 pre-burnin of  $1.0 \times 10^7$  generations. We used a 50% burnin and validated that all runs  
221 converged and that all ESS values were greater than 200 using Tracer 1.7.1 (Rambaut et  
222 al. 2018), and combined and summarized posterior tree sets into a maximum clade  
223 credibility tree with median node heights using LogCombiner v. 2.6.7 and TreeAnnotator  
224 v. 2.6.6 (Bouckaert et al. 2014; 2019).

225

226 **Taxonomy.** We developed a phylogenetic taxonomy of *Acipenseridae* following the  
227 principles of phylogenetic nomenclature outlined in the *PhyloCode* (de Queiroz and  
228 Gauthier 1990, 1992, 1994; Cantino and de Queiroz 2020). Following Recommendation  
229 6.1A in the International Code of Phylogenetic Nomenclature (*PhyloCode*) ver. 6  
230 (Cantino and de Queiroz 2020), we italicize all formal clade names. Following Articles  
231 9.5 and 9.9, the clades we name and review here are defined as minimum-crown-clades  
232 that have at minimum two internal specifiers that are both extant (Cantino and de Queiroz  
233 2020).

234

## 235 **Results**

236

237 **Phylogenetic Relationships of *Acipenseridae*.** Apart from the tip-dated Bayesian  
238 analysis of the morphological dataset, our analyses of different datasets resulted in  
239 largely congruent phylogenetic relationships of *Acipenseridae*. These results are also  
240 consistent with previous studies using the same molecular datasets (Luo et al. 2019;  
241 Shedko 2022; Birstein, Doukakis, and DeSalle 2002; Krieger et al. 2008; Shen et al.  
242 2020; Peng et al. 2007). The maximum likelihood phylogenies that we inferred using *cytb*  
243 (Figure 1), DNA sequences from 30 nuclear gene presented in Luo et al. (2019) (Figure  
244 2), and concatenated nuclear and mitochondrial sequences (Figure 3) resolve four major  
245 clades of *Acipenseridae*. The morphological dataset does not include any species of  
246 *Acipenser sensu stricto* (Figure 4). In all inferences of molecular datasets and analysis of  
247 the combined molecular and morphology dataset (Figures 1–3, 5), *Acipenser* Linnaeus

248 1758 *sensu stricto* is resolved as the sister to all other living species of *Acipenseridae* and  
249 includes the type species of *Acipenser*, *A. sturio* Linnaeus 1758, as well as the species *A.*  
250 *oxyrinchus* Mitchill 1815 and *A. desotoi* Vladykov 1955. A clade of Pacific species that  
251 were traditionally classified in *Acipenser* and *Huso* includes *Sinosturio dabryanus*  
252 (Duméril 1869), *Sinosturio medirostris* (Ayers 1854), *Sinosturio mikadoi* (Hilgendorf  
253 1892), *Sinosturio transmontanus* (Richardson 1836), *Sinosturio sinensis* (Gray 1835),  
254 *Sinosturio schrenckii* (Brandt 1869), and *Sinosturio dauricus* (Georgi 1775) and is  
255 resolved in the phylogenetic analyses of the nuclear genes (Figure 2), the analysis of the  
256 concatenated *cytb* and nuclear genes (Figure 3), and the fossil tip-dated relaxed clock  
257 analysis (Figure 5). The shovelnose sturgeons *Scaphirhynchus* Heckel 1836 and  
258 *Pseudoscaphirhynchus* Nikolskii 1900, each resolved as monophyletic, either form a  
259 grade leading to a clade of Atlantic species with uncertain phylogenetic relationships that  
260 are traditionally classified in *Acipenser* and *Huso* (Figures 2, 3, and 5) or bracket this  
261 clade such that *Pseudoscaphirhynchus* is nested within the Atlantic clade as sister to  
262 *Huso stellatus* (Pallas 1771) (Figure 1, Figure 4).

263 The phylogenetic resolution of *Pseudoscaphirhynchus* within *Acipenseridae* is the  
264 most noteworthy incongruence among phylogenies of sturgeons inferred using  
265 mitochondrial (Figure 1), nuclear (Figure 2), morphological (Figure 4), and concatenated  
266 nuclear and mitochondrial datasets (Figure 3). The Bayesian tip-dated phylogeny of  
267 *Acipenseridae* resolves *Pseudoscaphirhynchus* as the sister lineage of the Atlantic Clade,  
268 delimited here as *Huso* Brandt & Ratzeburg 1833, but places *Scaphirhynchus* as the sister  
269 lineage of a clade containing *Huso*, *Pseudoscaphirhynchus*, and the Pacific Clade  
270 delimited here as *Sinosturio* Jaekel in Weigelt (1929). There is strong support (posterior =  
271 1.0) for the placement of *Acipenser stellatus* in *Huso* (Figure 5) rather than as the sister  
272 species of *Pseudoscaphirhynchus* (Figure 1, Figure 4).

273

274 **Divergence Time Estimates.** The time-calibrated phylogenies from our Bayesian  
275 analyses of morphological and molecular characters produce different estimates of the  
276 timescale of acipenserid evolutionary history, although both relaxed clock analyses place  
277 the most recent common ancestor (MRCA) of *Acipenseridae* in the middle to Late  
278 Cretaceous. The relaxed clock tip-dating analysis of morphological data result in a

279 posterior estimated age of the MRCA of *Acipenseriformes* at 202.62 Ma (95% HPD:  
 280 148.89, 265.47 Ma), crown *Acipenseridae* originates at 84.3 Ma (95% HPD: 66.6, 108.77  
 281 Ma), and the clade consisting of all sturgeons to the exclusion of *Scaphirhynchus*  
 282 originates at 39.1 Ma (95% HPD: 13.92, 70.59 Ma). In the tip-dated relaxed clock  
 283 analysis using the concatenated mitochondrial and nuclear gene molecular data, the  
 284 estimated age of the MRCA of *Acipenseriformes* is 172.22 Ma (95% HPD: 128.88, 220.9  
 285 Ma). The age of the MRCA of *Acipenseridae* is 100.55 Ma (95% HPD: 71.34, 138.6  
 286 Ma). *Acipenser sensu stricto* (*A. sturio*, *A. oxyrinchus*, and *A. desotoi*) originates during the  
 287 latest Paleogene, 24.69 Ma (95% HPD: 1.7, 55.14 Ma). The MRCA of *Sinosturio* is dated  
 288 to the Eocene (median = 57.72 Ma, 95% HPD: 23.73, 87.29 Ma), as is the MRCA of  
 289 *Huso* (median = 53.06 Ma, 95% HPD: 30.32, 75.81 Ma). The MRCAs of  
 290 *Pseudoscaphirhynchus* (median = 9.02 Ma, 95% HPD: 0.36, 32.73 Ma) and  
 291 *Scaphirhynchus* (median = 5.86 Ma, 95% HPD: 0.1, 40.98 Ma) are both estimated as  
 292 Late Miocene in age.

293

## 294 **Taxonomy**

295

296 ***Acipenseridae* Bonaparte 1831 [C.D. Brownstein and T. J. Near], converted clade**  
 297 **name**

298 **Definition:** The least inclusive crown clade that contains *Acipenser sturio* Linnaeus  
 299 1758, *Huso huso* (Linnaeus 1758), and *Sinosturio dabryanus* (Duméril 1869). This is a  
 300 minimum-crown-clade definition.

301

302 **Registration number:** 1079

303

304 **Etymology:** *Acipenser* is the Latin name for sturgeon, which is derived from the ancient  
 305 Greek ἀκκίπηςσιος (Thompson 1947).

306

307 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
 308 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5). The extinct  
 309 species †*Protoscaphirhynchus squamosus* Wilimovsky 1956, known from a single

310 poorly-preserved specimen, is not included in the reference phylogeny; this taxon  
311 resolves as the sister species of *Scaphirhynchus* in phylogenies inferred from  
312 morphological characters (Grande and Bemis 1996:fig. 11; Grande and Hilton 2006:fig.  
313 30).

314

315 **Composition:** *Acipenseridae* includes 27 living species (Table 1; Fricke et al. 2023)  
316 classified in *Acipenser* Linnaeus 1758, *Huso* Brandt and Ratzeburg 1833, *Scaphirhynchus*  
317 Heckel 1836, *Pseudoscaphirhynchus* Nikolskii 1900, and *Sinosturio* Jaekel in Weigelt  
318 (1929). Fossil taxa of *Acipenseridae* include †*Protoscaphirhynchus squamosus*,  
319 †“*Acipenser*” *praeparatorum* Hilton and Grande 2023, and potentially  
320 †*Acipenser amnisinferos* Hilton and Grande 2023, though this lattermost species is only  
321 known from a single partial skull and has not been included in phylogenetic analyses. No  
322 new living species of *Acipenseridae* have been described in the past 10 years (Fricke et  
323 al. 2023).

324

325 **Diagnostic Apomorphies:** Morphological synapomorphies of *Acipenseridae* include (1)  
326 five rows of bony scutes or plates on trunk of body (Grande and Bemis 1991, 1996;  
327 Bemis et al. 1997; Findeis 1997; Artyukhin 2006; Grande and Hilton 2006; Hilton et al.  
328 2011), (2) mandibular sensory canal absent (Grande and Bemis 1991), (3) stout anterior  
329 spine of pectoral fin composed of fused fin rays (Grande and Bemis 1991, 1996; Bemis et  
330 al. 1997; Findeis 1997), (4) presence of a platelike supraorbital with a descending  
331 preorbital process (Grande and Bemis 1996; Grande and Hilton 2006; Hilton et al. 2011),  
332 (5) rostral canals arched, curving lateral to barbels (Grande and Bemis 1996; Bemis et al.  
333 1997; Findeis 1997; Hilton et al. 2011), (6) posterior cleithral notch present (Grande and  
334 Bemis 1996; Bemis et al. 1997; Findeis 1997; Grande and Hilton 2006; Hilton et al.  
335 2011), (7) supracleithral cartilage present (Findeis 1997; Hilton et al. 2011), (8)  
336 basipterygial process present (Findeis 1997), (9) palatal process present (Findeis 1997;  
337 Hilton et al. 2011), (10) hypobranchial I with an anterior shelf (Findeis 1997; Hilton et al.  
338 2011), (11) hypobranchial 3 makes a bicontact joint with basibranchial 1 (Findeis 1997),  
339 (12) ascending process of parasphenoid extends anteriorly, (13) individual elements of

340 branchiostegals are distinctly shaped (Hilton et al. 2011), and (14) trunk lateral line  
 341 encased in large scutes (Hilton et al. 2011).

342

343 **Synonyms:** *Sturionidae* (Owen 1846:50) is a partial synonym of *Acipenseridae*.

344

345 **Comments:** The extinct species †*Anchiacipenser acanthaspis* from the Campanian in  
 346 Alberta, Canada (Sato et al. 2018), †*Priscosturion longipinnis* from the Campanian in  
 347 Montana, USA (Grande and Hilton 2006, 2009), †*Engdahlichthys milviaegis* from the  
 348 Danian in Montana, USA (Murray et al. 2020), and †*Boreiosturion labyrinthicus* from  
 349 the Campanian in Alberta, Canada (Murray et al. 2023) have occasionally been classified  
 350 in *Acipenseridae*. Phylogenetic analyses of morphological characters consistently resolve  
 351 these fossil taxa outside of the crown *Acipenseridae* or in a polytomy along with several  
 352 lineages of *Acipenseridae* (Grande and Hilton 2006; Hilton and Forey 2009; Hilton et al.  
 353 2011; Sato et al. 2018; Shedko 2022; Murray et al. 2023). We treat these fossil taxa as  
 354 pan-acipenserids and they are not included in our delimitation of *Acipenseridae*.

355 Several morphological character states proposed as apomorphies for  
 356 *Acipenseridae* are diagnostic for a more inclusive pan-acipenserid clade that includes  
 357 †*Priscosturion longipinnis*. Possible synapomorphies for this acipenserid total clade  
 358 include the supracleithrum reaching the level of the extrascapulars (Grande and Bemis  
 359 1996; Findeis 1997; Hilton et al. 2011), the presence of a cardiac shield (Grande and  
 360 Bemis 1996; Findeis 1997; Hilton et al. 2011), a pillar-like and laterally concave  
 361 dorsalmost branchiostegal (Findeis 1997; Hilton et al. 2011), and a suture between  
 362 clavicle and cleithrum is interdigitating (Findeis 1997; Hilton et al. 2011). The presence  
 363 of supracleithral cartilage may be an apomorphy for *Acipenseridae*, but its absence in  
 364 fossil pan-acipenserids might be a preservational artifact (Hilton et al. 2011).

365 *Acipenseridae* is a valid family-group name under the *International Code of*  
 366 *Zoological Nomenclature* (Van der Laan et al. 2014:27).

367

368 **Constituent Lineages:**

*Acipenser*

*Huso*

*Pseudoscaphirhynchus*

*Scaphirhynchus*

*Sinosturio*

†“*Acipenser*” *praepparatorum*

†*Protoscaphirhynchus*

369

370 ***Acipenser* Linnaeus 1758 [C.D. Brownstein and T. J. Near], converted clade name**

371

372 **Definition:** The least inclusive crown clade that contains *Acipenser sturio* Linnaeus  
373 1758, *Acipenser oxyrinchus* Mitchill 1815, and *Acipenser desotoi* Vladykov 1955. This is  
374 a minimum-crown-clade definition.

375

376 **Registration number:** 1080

377

378 **Etymology:** *Acipenser* is the Latin name for sturgeon, which is derived from the ancient  
379 Greek ἀκκιπήσιος (Thompson 1947).

380

381 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
382 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5).

383

384 **Composition:** *Acipenser* includes three living species *Acipenser desotoi* Vladykov 1955  
385 Gulf Sturgeon, *Acipenser oxyrinchus* Mitchill 1815 Atlantic Sturgeon, and *Acipenser*  
386 *sturio* Linnaeus 1758 European Sea Sturgeon (Table 1).

387

388 **Diagnostic Apomorphies:** There are no known morphological synapomorphies for  
389 *Acipenser*; however, in a parsimony analysis of morphological characters, the reduction  
390 of the bulb-shaped sack of the stomach resolves *Acipenser* as monophyletic (Artyukhin  
391 2006). This trait is also present in *Huso huso* and all species of *Sinosturio* except *S.*  
392 *schrenckii* (Artyukhin 2006).

393

394 **Synonyms:** *Antaceus* (Fitzinger and Heckel 1836:292–293) and *Dinoctus* (Rafinesque  
395 1818:447) are unambiguous synonyms of *Acipenser*. *Gladostomus* (Holly 1936:31),  
396 *Helopes* (Brandt and Ratzeburg 1833:3), *Lioniscus* (Fitzinger and Heckel 1836:270), and  
397 *Shipa* (Brandt 1869:113) are partial synonyms of *Acipenser*.

398

399 **Comments:** In molecular phylogenies, *Acipenser* is consistently resolved as a clade and  
 400 often as the sister lineage of all other *Acipenseridae* (Figures 1, 2, 3, and 5; Birstein and  
 401 DeSalle 1998; Fontana et al. 2001; Ludwig et al. 2001; Birstein et al. 2002; Krieger et al.  
 402 2008; Laumann 2016; Luo et al. 2019; Shen et al. 2020; Cheng et al. 2021; Shedko 2022;  
 403 Tsessarsky 2022). The monophyly of *Acipenser* is not supported in a set of phylogenetic  
 404 analyses using 62 morphological characters (Hilton and Forey 2009; Hilton et al. 2011;  
 405 Sato et al. 2018; Murray et al. 2023), but *Acipenser* is resolved as a clade in a maximum  
 406 parsimony analysis of 28 morphological characters (Artyukhin 2006).

407 The North American species *Acipenser oxyrinchus* and *A. desotoi* are  
 408 allopatrically distributed along the Atlantic Slope and eastern Gulf of Mexico (Vladykov  
 409 1955; Vladykov and Greeley 1963; Gruchy and Parker 1980c; Smith 1985:47; Jenkins  
 410 and Burkhead 1994:187; Boschung and Mayden 2004:107; Wilson and McKinley 2004;  
 411 Rohde et al. 2009:71–72; Kuhajda 2014; Robins et al. 2018:42–44). *Acipenser desotoi*  
 412 was initially described as a subspecies of *A. oxyrinchus* (Vladykov 1955). However,  
 413 subsequent analysis of morphological differences and the presence of species-specific  
 414 mtDNA haplotypes support the recognition of the Atlantic Sturgeon and Gulf Sturgeon as  
 415 distinct species (Wooley 1985; Ong et al. 1996).

416 *Acipenser* is a valid genus-group name under the *International Code of*  
 417 *Zoological Nomenclature* that was historically applied to a group of 18 species of  
 418 *Acipenseridae* (Eschmeyer and Fricke 2024). Given the non-monophyly of this previous  
 419 delimitation of *Acipenser*, we limit the group to three species (Table 1; Figures 1, 2, 3,  
 420 and 5). *Acipenser sturio* Linnaeus 1758 is the type species of *Acipenser*.

421

422 **Constituent Species:**

*Acipenser desotoi*    *Acipenser oxyrinchus*    *Acipenser sturio*

423

424 ***Sinosturio* Jaekel in Weigelt 1929 [T. J. Near and C.D. Brownstein], converted clade**  
 425 **name**

426

427 **Definition:** The least inclusive crown clade that contains *Sinosturio transmontanus*  
428 (Richardson 1836), *Sinosturio medirostris* (Ayers 1854), and *Sinosturio dabryanus*  
429 (Duméril 1869). This is a minimum-crown-clade definition.

430

431 **Registration number:** 1081

432

433 **Etymology:** *Sinosturio* is from the French sino pertaining to China and the Latin sturio,  
434 which means sturgeon.

435

436 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
437 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5).

438

439 **Composition:** *Sinosturio* includes seven living species: *Sinosturio dabryanus* (Duméril  
440 1869) Yangtze Sturgeon, *Sinosturio dauricus* (Georgi 1775) Kaluga, *Sinosturio*  
441 *medirostris* (Ayers 1854) Green Sturgeon, *Sinosturio mikadoi* (Hilgendorf 1892)  
442 Sakhalin Sturgeon, *Sinosturio schrenckii* (Brandt 1869) Japanese Sturgeon, *Sinosturio*  
443 *sinensis* (Gray 1835) Chinese Sturgeon, and *Sinosturio transmontanus* (Richardson 1836)  
444 White Sturgeon (Table 1).

445

446 **Diagnostic Apomorphies:** Characters that may be synapomorphies of *Sinosturio* include  
447 (1) a wide rostrum (Artyukhin 2006) and (2) the presence of large and rounded fontanelle  
448 positioned between frontal bones (Artyukhin 2006). These traits are not present in *S.*  
449 *dauricus* and *S. schrenckii* (Artyukhin 2006).

450

451 **Synonyms:** There are no synonyms of *Sinosturio*.

452

453 **Comments:** In molecular phylogenies, species of *Sinosturio* are resolved as a  
454 monophyletic group that is distantly related to species of *Acipenser* and *Huso* (Figures 1,  
455 2, 3, and 5; Ludwig et al. 2001; Dillman et al. 2007; Krieger et al. 2008; Laumann 2016;  
456 Cheng et al. 2021; Shedko 2022).



457 Species of *Sinosturio* are distributed in the North Pacific of Asia and North  
 458 America (Lee 1980a, b; Bemis et al. 1997; Wei et al. 1997; Billard and Lecointre 2000;  
 459 Wilson and McKinley 2004). Species of *Sinosturio* have been referred as the Pacific  
 460 Clade in previous phylogenetic analyses (Luo et al. 2019).

461 *Sinosturio* is a valid genus-group name under the *International Code of*  
 462 *Zoological Nomenclature*. Given the non-monophyly of the previous delimitations of  
 463 *Acipenser* and *Huso*, *Sinosturio* was chosen because it is the oldest available group name  
 464 among species resolved in this clade. *Sinosturio dabryanus* (Duméril 1869) is the type  
 465 species of *Sinosturio*.

466

467 **Constituent Species:**

<i>Sinosturio dabryanus</i>	<i>Sinosturio dauricus</i>	<i>Sinosturio medirostris</i>
<i>Sinosturio mikadoi</i>	<i>Sinosturio schrenckii</i>	<i>Sinosturio sinensis</i>
<i>Sinosturio transmontanus</i>		

468

469 ***Huso* Brandt and Ratzeburg 1833 [C.D. Brownstein and T. J. Near], converted clade**  
 470 **name**

471

472 **Definition:** The least inclusive crown clade that contains *Huso huso* (Linnaeus 1758),  
 473 *Huso fulvescens* (Rafinesque 1817), and *Huso gueldenstaedtii* (Brandt and Ratzeburg  
 474 1833). This is a minimum-crown-clade definition.

475

476 **Registration number:** 1082

477

478 **Etymology:** *Huso* is a Medieval Latin and Old High German word for sturgeon (Scharpf  
 479 2024).

480

481 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
 482 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5).

483

484 **Composition:** *Huso* includes 11 living species: *Huso baerii* (Brandt 1869) Siberian  
 485 Sturgeon, *Huso brevirostrum* (Lesueur 1818) Shortnose Sturgeon, *Huso colchicus* (Marty  
 486 1940) Colchian Sturgeon, *Huso fulvescens* (Rafinesque 1817) Lake Sturgeon, *Huso*  
 487 *gueldenstaedtii* (Brandt and Ratzeburg 1833) Russian Sturgeon, *Huso huso* (Linnaeus  
 488 1758) Beluga, *Huso naccarii* (Bonaparte 1836) Adriatic Sturgeon, *Huso nudiventris*  
 489 (Lovetsky 1828) Ship Sturgeon, *Huso persicus* (Borodin 1897) Persian Sturgeon, *Huso*  
 490 *ruthenus* (Linnaeus 1758) Sterlet, and *Huso stellatus* (Pallas 1771) Starry Sturgeon  
 491 (Table 1).

492

493 **Diagnostic Apomorphies:** There are no known morphological synapomorphies for  
 494 *Huso*. However, two characters are of note (1) numerous distinct prominences on the  
 495 surfaces of ventral rostral bones are present in *H. huso*, *H. ruthenus*, and *H. baerii* but not  
 496 *H. stellatus*, *H. brevirostrum*, and *H. fulvescens* (Hilton and Forey 2009; Hilton et al.  
 497 2011) and (2) a slight medial broadening of the dermopalatine is present in *H. huso*, *H.*  
 498 *ruthenus*, *H. brevirostrum*, and *H. fulvescens* but not in *H. stellatus* and *H. baerii* (Hilton  
 499 and Forey 2009; Hilton et al. 2011). A medially broadened dermopalatine is also present  
 500 in species of *Scaphirhynchus* and in †*Priscosturion longipinnis*. The presence of these  
 501 traits are not known for *Huso nudiventris*, *H. persicus*, *H. gueldenstaedtii*, *H. colchicus*,  
 502 and *H. naccarii* because these species were not included in the morphological  
 503 phylogenetic analyses (Hilton and Forey 2009; Hilton et al. 2011).

504

505 **Synonyms:** *Antacea* (Bory de Saint-Vincent 1822:410) is a synonym of *Huso*.

506

507 **Comments:** *Huso* is resolved as monophyletic and the sister lineage of  
 508 *Pseudoscaphirhynchus* in phylogenetic analyses of DNA sequences from nuclear genes  
 509 and concatenated mtDNA and nuclear genes (Figures 2, 3, and 5; Luo et al. 2019).  
 510 Phylogenies inferred from mtDNA gene sequences consistently nest  
 511 *Pseudoscaphirhynchus* within *Huso* as the sister lineage of *H. stellatus* (Figure 1; Birstein  
 512 et al. 2002; Dillman et al. 2007; Laumann 2016; Shedko 2022). *Huso stellatus* and  
 513 *Pseudoscaphirhynchus* are resolved as a clade in morphological phylogenetic analyses on  
 514 the basis of the horizontal arm of the jugal undercutting the nasal capsule (Doukakis

515 2000; Hilton and Forey 2009; Hilton et al. 2011; Sato et al. 2018; Hilton et al. 2022;  
516 Murray et al. 2023).

517         There remains uncertainty in the delimitation of some species of *Huso*. Molecular  
518 phylogenies inferred from mtDNA and SNPs resolve *Huso baerii* as the sister lineage of  
519 a clade containing *H. gueldenstaedtii*, *H. naccarii*, and *H. persicus* (Figure 1; Ludwig et  
520 al. 2001; Birstein et al. 2002; Dillman et al. 2007; Krieger et al. 2008; Rastorguev et al.  
521 2008; Rastorguev et al. 2013; Laumann 2016; Cheng et al. 2021; Shedko 2022). In  
522 contrast, phylogenetic analyses of nuclear genes resolve *H. baerii* and *H. ruthenus* as  
523 sister species (Figure 2; Luo et al. 2019). Historically, *H. baerii* comprised three  
524 subspecies (Ruban 1997): the nominate *H. b. baerii*, *H. b. stenorrhynchus* (Nikolskii  
525 1896), and *H. b. baicalensis* (Nikolskii 1896). The subspecies are not distinct in analysis  
526 of mtDNA, but the population of *H. baerii* in Lake Baikal contains several mtDNA  
527 haplotypes not shared with other populations (Doukakis et al. 1999; Birstein et al. 2009).  
528 The species *H. colchicus*, *H. naccarii*, and *H. persicus* have been considered in various  
529 combinations as subspecies of *H. gueldenstaedtii* or *H. persicus* (Birstein and Bemis  
530 1997; Ruban et al. 2008, 2011; Vasil'eva and Vasil'ev 2021), but all are treated as  
531 distinct species here (Table 1; Vecsei and Artyukhin 2001; Eschmeyer and Fricke 2024).  
532 Phylogenetic analysis of mtDNA gene sequences does not resolve specimens of *H.*  
533 *gueldenstaedtii*, *H. persicus*, *H. colchicus*, nor *H. naccarii* as reciprocally monophyletic  
534 lineages (Birstein et al. 2000; Doukakis et al. 2005; Ruban et al. 2008, 2011).  
535 Morphometric variation and differential timing of spawning in sympatry are cited as  
536 evidence for the distinctiveness of *H. gueldenstaedtii* and *H. persicus* (Vasil'eva and  
537 Vasil'ev 2021). Complicating the delimitation of species of *Huso* is the likely mtDNA  
538 introgression between *H. baerii* and species of the *H. gueldenstaedtii* complex and the  
539 exceptionally slow rate of molecular evolution in *Acipenseriformes* (Jenneckens et al.  
540 2000; Rastorguev et al. 2008; Rastorguev et al. 2013; Brownstein et al. 2024).

541         Species of *Huso* are distributed in the Caspian Sea, Black Sea, Aral Sea, Aegean  
542 Sea, Adriatic Sea, the Siberian Sea, the Atlantic Coast of North America, Mississippi  
543 River system, Great Lakes, and Hudson Bay (Gruchy and Parker 1980a, b; Pirogovskii et  
544 al. 1989; Shubina et al. 1989; Sokolov and Vasil'ev 1989a, c, b; Tortonese 1989;  
545 Vlasenko et al. 1989a; Vlasenko et al. 1989b; Bemis et al. 1997; Billard and Lecointre

546 2000; Wilson and McKinley 2004). Species of *Huso* have been referred as the Atlantic  
547 Clade in previous phylogenetic analyses (Luo et al. 2019).

548 *Huso* is a valid genus-group name under the *International Code of Zoological*  
549 *Nomenclature*. Historically, *Huso* was applied to a group containing two species  
550 (Eschmeyer and Fricke 2024) that are not resolved as monophyletic (Figures 1, 2, 3, and  
551 5). *Huso huso* (Linnaeus 1758) is the type species of *Huso*.

552

553 **Constituent Species:**

<i>Huso baerii</i>	<i>Huso brevirostrum</i>	<i>Huso colchicus</i>
<i>Huso fulvescens</i>	<i>Huso gueldenstaedtii</i>	<i>Huso huso</i>
<i>Huso naccarii</i>	<i>Huso nudiventris</i>	<i>Huso persicus</i>
<i>Huso ruthenus</i>	<i>Huso stellatus</i>	

554

555 ***Scaphirhynchus* Heckel 1836 [C.D. Brownstein and T. J. Near], converted clade**  
556 **name**

557

558 **Definition:** The least inclusive crown clade that contains *Scaphirhynchus platyrhynchus*  
559 (Rafinesque 1820), *Scaphirhynchus albus* (Forbes and Richardson 1905), and  
560 *Scaphirhynchus suttkusi* Williams and Clemmer 1991. This is a minimum-crown-clade  
561 definition.

562

563 **Registration number:** 1083

564

565 **Etymology:** From the ancient Greek σκαφίς (sk'eífiz) meaning spade or shovel, and  
566 ῥύγχος (r'agkoōz) meaning the snout or muzzle of a mammal or the beak of a bird.

567

568 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
569 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5).

570

571 **Composition:** *Scaphirhynchus* includes three living species: *Scaphirhynchus albus*  
572 (Forbes and Richardson 1905) Pallid Sturgeon, *Scaphirhynchus platyrhynchus*

573 (Rafinesque 1820) Shovelnose Sturgeon, and *Scaphirhynchus suttkusi* Williams and  
 574 Clemmer 1991 Alabama Sturgeon (Table 1).

575

576 **Diagnostic Apomorphies:** Morphological synapomorphies of *Scaphirhynchus* include  
 577 (1) caudal peduncle and preanal area armored with scutes (Mayden and Kuhajda 1996;  
 578 Findeis 1997; Kuhajda 2002), (2) flattened and elongate caudal peduncle (Mayden and  
 579 Kuhajda 1996; Findeis 1997; Kuhajda 2002), (3) presence of preorbital spines (Mayden  
 580 and Kuhajda 1996; Kuhajda 2002), (4) presence of accessory fringe on barbel (Mayden  
 581 and Kuhajda 1996; Kuhajda 2002), (5) lower lip with four lobes (Mayden and Kuhajda  
 582 1996; Kuhajda 2002), (6) lower lip continuous or narrowly interrupted medially (Mayden  
 583 and Kuhajda 1996; Kuhajda 2002), (7) incompletely developed clavicle keel (Mayden  
 584 and Kuhajda 1996), (8) lateral extrascapulars are clustered laterally alongside the median  
 585 extrascapular (Findeis 1997), (10) complete circumorbital present (Findeis 1997), (11)  
 586 branchiostegal 1 short and triangular (Findeis 1997), (12) crenulated gill rakers (Findeis  
 587 1997), (13) cleithral wall present (Findeis 1997), (14) propterygial fossa encircled by a  
 588 thin process (Findeis 1997), (15) coracoid shelf restricted to the cleithrum (Findeis 1997),  
 589 (16) dermopalatine and ectopterygoid fused (Findeis 1997; Hilton et al. 2011), (17)  
 590 elongate caudal fin element present (Grande and Hilton 2006), (18) supraorbital bone  
 591 present with an considerably enlarged descending process (Hilton et al. 2011), (19) dorsal  
 592 head of hyomandibular is circular in cross section (Hilton et al. 2011), and (20) the  
 593 anterior junction of clavicles forms a straight line (Hilton et al. 2011).

594

595 **Synonyms:** *Parascaphirhynchus* (Forbes and Richardson 1905:38) and *Scaphyrhynchops*  
 596 Gill in Hayden (1863:178) are unambiguous synonyms of *Scaphirhynchus*.

597

598 **Comments:** *Scaphirhynchus* is consistently resolved as monophyletic in analyses of  
 599 morphological and molecular data (Mayden and Kuhajda 1996; Billard and Lecointre  
 600 2000; Ludwig et al. 2001; Birstein et al. 2002; Dillman et al. 2007; Peng et al. 2007;  
 601 Krieger et al. 2008; Laumann 2016; Shen et al. 2020; Cheng et al. 2021; Shedko 2022).  
 602 Phylogenetic analyses resolve every possible relationship among the three species of  
 603 *Scaphirhynchus*: morphology and mtDNA genes resolve *S. suttkusi* and *S. platorynchus*

604 as sister species (Mayden and Kuhajda 1996; Ludwig et al. 2001; Birstein et al. 2002;  
 605 Peng et al. 2007), analysis of combined morphological and mtDNA datasets, whole  
 606 mtDNA genomes, and 77 single nucleotide polymorphisms resolve *S. platorynchus* and  
 607 *S. albus* as sister species (Birstein et al. 2002; Laumann 2016; Zhou et al. 2022), and  
 608 phylogenetic analysis of whole mtDNA genomes resolve *S. suttkusi* and *S. albus* as sister  
 609 species (Shen et al. 2020; Cheng et al. 2021).

610 Meristic and morphometric traits provided evidence for the discovery,  
 611 delimitation, and description of the three species of *Scaphirhynchus* (Forbes and  
 612 Richardson 1905; Bailey and Cross 1954; Williams and Clemmer 1991; Keenlyne et al.  
 613 1994; Mayden and Kuhajda 1996; Kuhajda 2002). Relationships among the species of  
 614 *Scaphirhynchus* are unresolved and the species *S. platorynchus* and *S. albus* are not  
 615 reciprocally monophyletic in phylogenetic trees inferred from mtDNA sequences  
 616 (Simons et al. 2001; Dillman et al. 2007). This lack of reciprocal monophyly is reflected  
 617 by the lack of fixed genetic differences among the species of *Scaphirhynchus* (Phelps and  
 618 Allendorf 1983; Campton et al. 2000; Tranah et al. 2001; Schrey et al. 2007; Eichelberger  
 619 et al. 2014), but one allele at a single microsatellite locus is fixed for *S. suttkusi* (Ray et  
 620 al. 2007).

621 *Scaphirhynchus* is a valid genus-group name under the *International Code of*  
 622 *Zoological Nomenclature* and was applied to a group containing *S. platorynchus* and *S.*  
 623 *albus* (Bailey and Cross 1954), which was later expanded to include *S. suttkusi* (Williams  
 624 and Clemmer 1991). *Scaphirhynchus platorynchus* (Rafinesque 1820) is the type species  
 625 of *Scaphirhynchus*.

626

627 **Constituent Species:**

*Scaphirhynchus albus* *Scaphirhynchus platorynchus* *Scaphirhynchus suttkusi*

628

629 ***Pseudoscaphirhynchus Nikolskii* 1900 [T. J. Near and C.D. Brownstein], converted**  
 630 **clade name**

631

632 **Definition:** The least inclusive crown clade that contains *Pseudoscaphirhynchus*  
 633 *fedtschenkoi* (Kessler 1872), *Pseudoscaphirhynchus hermanni* (Kessler 1877), and

634 *Pseudoscaphirhynchus kaufmanni* (Kessler 1877). This is a minimum-crown-clade  
635 definition.

636

637 **Registration number:** 1084

638

639 **Etymology:** From the ancient Greek ψεῦδος (s'u:dōŭ) meaning a lie or falsehood, σκαφίς  
640 (sk'eĩfız) meaning spade or shovel, and ῥύγχος (r'agkoŭz) meaning snout or muzzle of a  
641 mammal or beak of a bird.

642

643 **Reference Phylogeny:** A phylogeny inferred from a concatenated DNA sequence dataset  
644 containing a mitochondrial (*cytb*) gene and 30 nuclear genes (Figure 5).

645

646 **Composition:** *Pseudoscaphirhynchus* includes three living species:

647 *Pseudoscaphirhynchus fedtschenkoi* (Kessler 1872) Syr Darya Shovelnose Sturgeon,

648 *Pseudoscaphirhynchus hermanni* (Kessler 1877) Small Amu Darya Shovelnose Sturgeon,

649 and *Pseudoscaphirhynchus kaufmanni* (Kessler 1877) Amu Darya Shovelnose Sturgeon

650 (Table 1).

651

652 **Diagnostic Apomorphies:** Morphological synapomorphies of *Pseudoscaphirhynchus*  
653 include (1) presence of spikes on the frontal bones (Findeis 1997), (2) the trunk, occipital,  
654 and supratemporal canals are enclosed by the lateral extrascapulars (Findeis 1997), (3)  
655 the jugal is very large in size and lacks a canal process (Findeis 1997), (4) gill rakers are  
656 distally split with paired pronged tips (Findeis 1997), (5) tips of the clavicles meet as an  
657 anteromedial wedge (Findeis 1997), and (6) the caudal peduncle armored with irregularly  
658 arranged scutes positioned dorsal and ventral to the lateral line scutes (Hilton et al. 2011).

659

660 **Synonyms:** *Hemiscaphirhynchus* (Berg 1911) and *Kessleria* (Jordan 1905) are  
661 unambiguous synonyms of *Pseudoscaphirhynchus*.

662

663 **Comments:** *Pseudoscaphirhynchus* is resolved as monophyletic in analyses of  
664 morphological and molecular data (Billard and Lecointre 2000; Birstein et al. 2002;

665 Dillman et al. 2007; Hilton and Forey 2009; Nedoluzhko et al. 2020; Shen et al. 2020;  
 666 Shedko 2022), but some analyses of morphological characters have resolved  
 667 *Pseudoscaphirhynchus* as paraphyletic relative to *Scaphirhynchus* (Mayden and Kuhajda  
 668 1996; Kuhajda 2002). Within *Pseudoscaphirhynchus*, phylogenetic analysis of mtDNA  
 669 resolves the possibly extinct *P. fedtschenkoi* as the sister lineage of a clade consisting of  
 670 *P. hermanni* and *P. kaufmanni* (Nedoluzhko et al. 2020). The sympatric  
 671 *Pseudoscaphirhynchus hermanni* and *P. kaufmanni* are both endemic to the Amu Darya  
 672 River and are both critically endangered due to the Aral Sea ecological disaster  
 673 (Zholdasova 1997; Nedoluzhko et al. 2020). Mitochondrial DNA gene trees do not  
 674 resolve the syntopic species *P. hermanni* and *P. kaufmanni* as reciprocally monophyletic,  
 675 but both species are diagnosed by the presence or absence of rostral spines, caudal  
 676 filaments, and a skin fold at the anterior edge of the pectoral fin (Nedoluzhko et al. 2020).  
 677 *Pseudoscaphirhynchus* is a valid genus-group name under the *International Code*  
 678 *of Zoological Nomenclature* and was applied to a group containing *S. platorynchus* and *S.*  
 679 *albus* (Bailey and Cross 1954), which was later expanded to include *S. suttkusi* (Williams  
 680 and Clemmer 1991). *Pseudoscaphirhynchus hermanni* (Kessler 1877) is the type species  
 681 of *Pseudoscaphirhynchus*.

682

### 683 **Constituent Species:**

<i>Pseudoscaphirhynchus</i>	<i>Pseudoscaphirhynchus</i>	<i>Pseudoscaphirhynchus</i>
<i>fedtschenkoi</i>	<i>hermanni</i>	<i>kaufmanni</i>

684

685

### 686 **Discussion**

687 Our phylogenetic analyses of sturgeons, using both morphological and molecular  
 688 data, corroborate previous studies indicating that the traditional classifications of  
 689 *Acipenser* and *Huso* are not monophyletic (Figures 1, 2, 3, 4, and 5; Birstein et al. 2002;  
 690 Dillman et al. 2007; Peng et al. 2007; Krieger et al. 2008; Hilton et al. 2011; Sato et al.  
 691 2018; Luo et al. 2019; Shen et al. 2020; Shedko 2022). This non-monophyly has been  
 692 recognized for over a decade, with Hilton et al. (2011:157) asserting that "the current  
 693 classification of extant members of Acipenseridae does not reflect the phylogenetic



694 relationships within the family as they are currently understood." Given the consistent  
695 evidence for non-monophyly of *Acipenser* and *Huso*, we propose revisions to the  
696 taxonomy of *Acipenseridae*. These changes include redefining both genera and elevating  
697 *Sinosturio* from synonymy with *Acipenser*. Taxonomy serves as the primary framework  
698 for organizing our understanding of biodiversity, and biological classifications should  
699 accurately represent phylogenetic relationships. Systematic studies produce phylogenies  
700 and taxonomies that form the foundation for evolutionary and comparative interpretations  
701 of biological information. Our proposed taxonomy of sturgeons aims to align with the  
702 inferred phylogenetic relationships within this clade.

703         The lineages *Scaphirhynchus* and *Pseudoscaphirhynchus* were traditionally  
704 classified in the *Scaphirhynchinae* or *Scaphirhynchini* (Bailey and Cross 1954; Sokolov  
705 and Berdichevski 1989; Mayden and Kuhajda 1996; Bemis et al. 1997; Findeis 1997).  
706 However, this group is not monophyletic (Figures 1, 3, 4, and 5). There is incongruence  
707 among the phylogenies that we infer using different types of molecular data: the mtDNA  
708 gene tree resolves *Pseudoscaphirhynchus* nested in *Huso*, but the phylogenies inferred  
709 from solely nuclear genes or concatenated mtDNA and nuclear genes resolve  
710 *Pseudoscaphirhynchus* and *Huso* as sister lineages (Figures 2 and 3). In addition to a  
711 number of proposed shared morphological character states (Findeis 1997; Artyukhin  
712 2006), other traits common to *Scaphirhynchus* and *Pseudoscaphirhynchus* include a  
713 relatively small body size, fan-shaped gill rakers, spines at the tip of the snout, and a flat  
714 spade-shaped snout that are likely the result of convergent evolution associated with  
715 adaptation to large river habitats (Mayden and Kuhajda 1996).

716         *Huso stellatus* and *Pseudoscaphirhynchus* are resolved as a clade in phylogenies  
717 inferred from mtDNA and morphology (Figures 1 and 4; Birstein et al. 2002; Dillman et  
718 al. 2007; Krieger et al. 2008; Hilton and Forey 2009; Hilton et al. 2011; Laumann 2016;  
719 Shedko 2022; Tsessarsky 2022). Phylogenies inferred from DNA sequences of nuclear  
720 genes resolve *Pseudoscaphirhynchus* as the sister lineage of all sampled species of *Huso*  
721 (Figure 2; Luo et al. 2019). The incongruence between the mtDNA gene tree and nuclear  
722 gene phylogeny may have resulted from ancient mitochondrial introgression from a  
723 lineage of *Huso* to the common ancestor of *Pseudoscaphirhynchus*. Phylogenetic  
724 inferences from morphology may be complicated by substantial within species variation

725 in skeletal features, as observed in *H. brevirostrum* (Hilton and Bemis 1999; Hilton et al.  
726 2011).

727         Hybridization is common among species of *Huso*, *Scaphirhynchus*, and  
728 *Pseudoscaphirhynchus* in natural conditions (Birstein et al. 1997; Tranah et al. 2004), and  
729 a number of intergeneric hybrids, e.g., *Huso naccarii* X *Acipenser transmontana*, *Huso*  
730 *baerii* X *Sinosturio schrenckii*, and *Sinosturio dabryanus* X *Huso baerii*, have been  
731 produced in aquaculture settings (Congiu et al. 2001; Ludwig et al. 2002; Bi et al. 2023).  
732 Detection of F2 individuals from hybrid crosses of species *Huso* and *Sinosturio* indicate  
733 these intergeneric hybrids are both viable and fertile (Zhang et al. 2013). The ability of  
734 lineages with a time to common ancestry exceeding 75 million years ago to produce  
735 viable and fit hybrids is likely associated with the very slow molecular evolutionary rate  
736 exhibited in *Acipenseriformes* (Brownstein et al. 2024) Amazingly, F1 hybrids were  
737 successfully produced from the artificial cross *Polyodon spathula* X *Acipenser*  
738 *gueldenstaedtii* (Káldy et al. 2020), two lineages that last shared common ancestry ~180-  
739 200 Ma during the Early Jurassic (Figures 4 and 5; Peng et al. 2007; Shen et al. 2020;  
740 Shedko 2022). Mitochondrial introgression is reported between *Huso gueldenstaedtii* and  
741 *H. baerii* (Rastorguev et al. 2013) and is likely more widespread among living lineages  
742 of sturgeons given the frequency of hybridization in the clade and the apparent lack of  
743 postzygotic reproductive incompatibilities among the most distantly related species of  
744 sturgeons.

745         Our proposed taxonomy of sturgeons provides a classification framework that  
746 agrees with inferred phylogenetic relationships of *Acipenseridae*. Given that  
747 overharvesting and degradation of aquatic habitats have negatively impacted sturgeons  
748 and all species are threatened or endangered, an understanding of phylogenetic  
749 relationships and a taxonomy that reflects the phylogeny is crucial for the effective  
750 management and investigation of the biology of these imperiled species (Hilton et al.  
751 2011).

752

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1429  
1430



## Figure Legends

### **Figure 1. Maximum Likelihood Phylogeny of Sturgeons Using Mitochondrial DNA.**

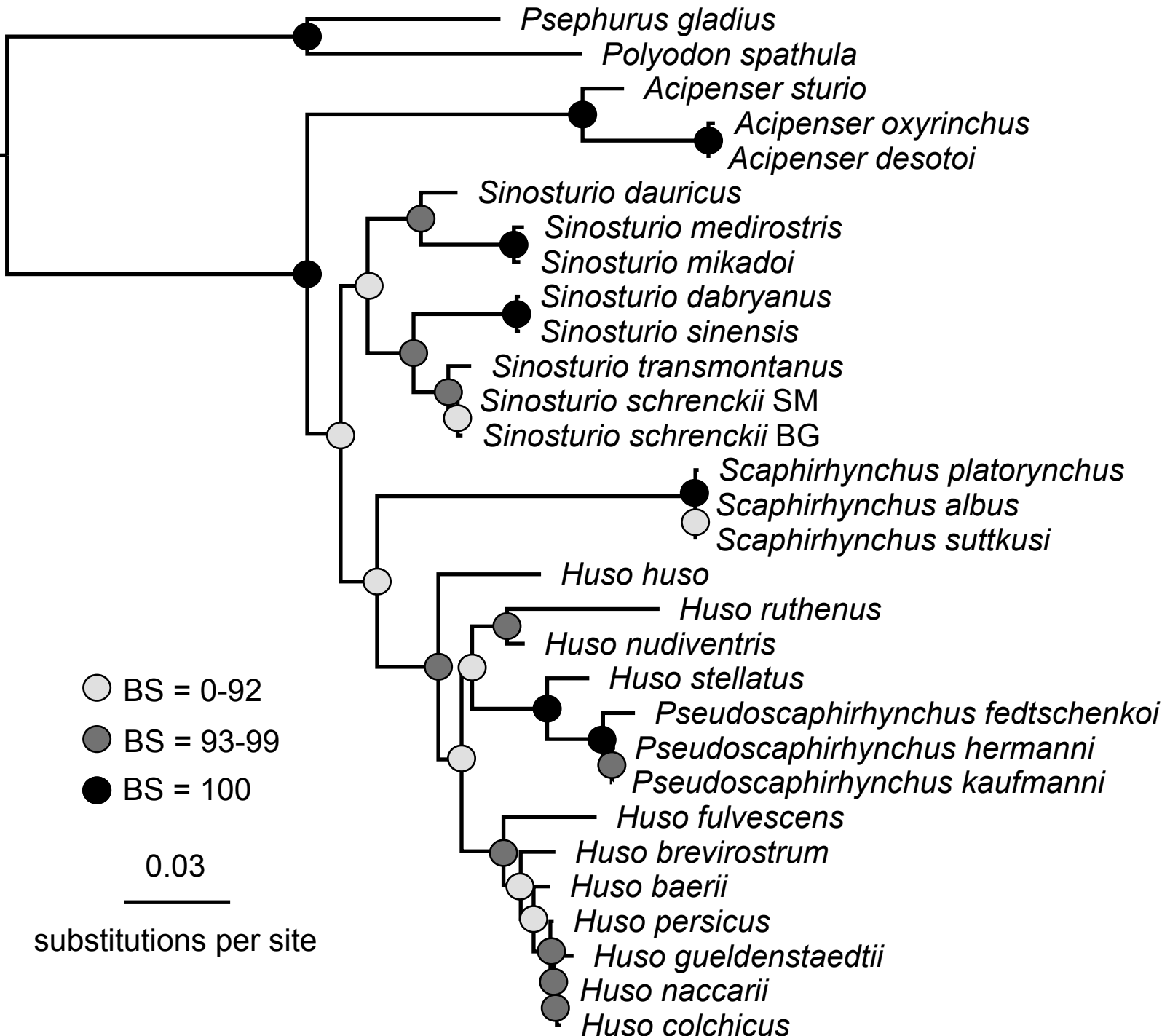
Maximum likelihood phylogeny generated in IQ-TREE 2 using aligned *cytb* sequences for 27 species of sturgeons and two species of paddlefishes. Numbers at nodes are ultrafast bootstrap supports.

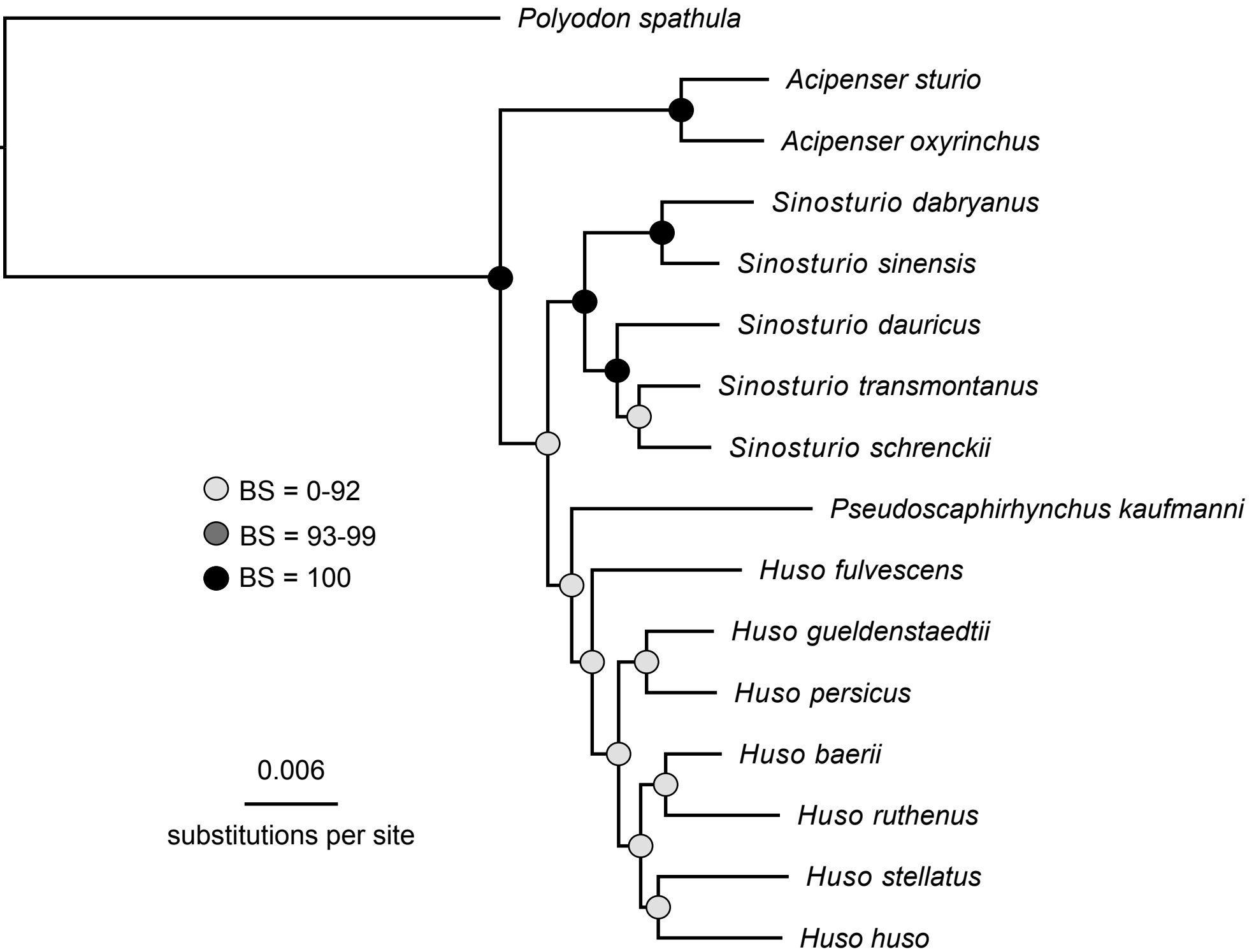
**Figure 2. Maximum Likelihood Phylogeny of Sturgeons Using Nuclear DNA.** Maximum likelihood phylogeny generated in IQ-TREE 2 using aligned sequences of 30 nuclear markers for 16 species of sturgeons and paddlefishes. Numbers at nodes are ultrafast bootstrap supports.

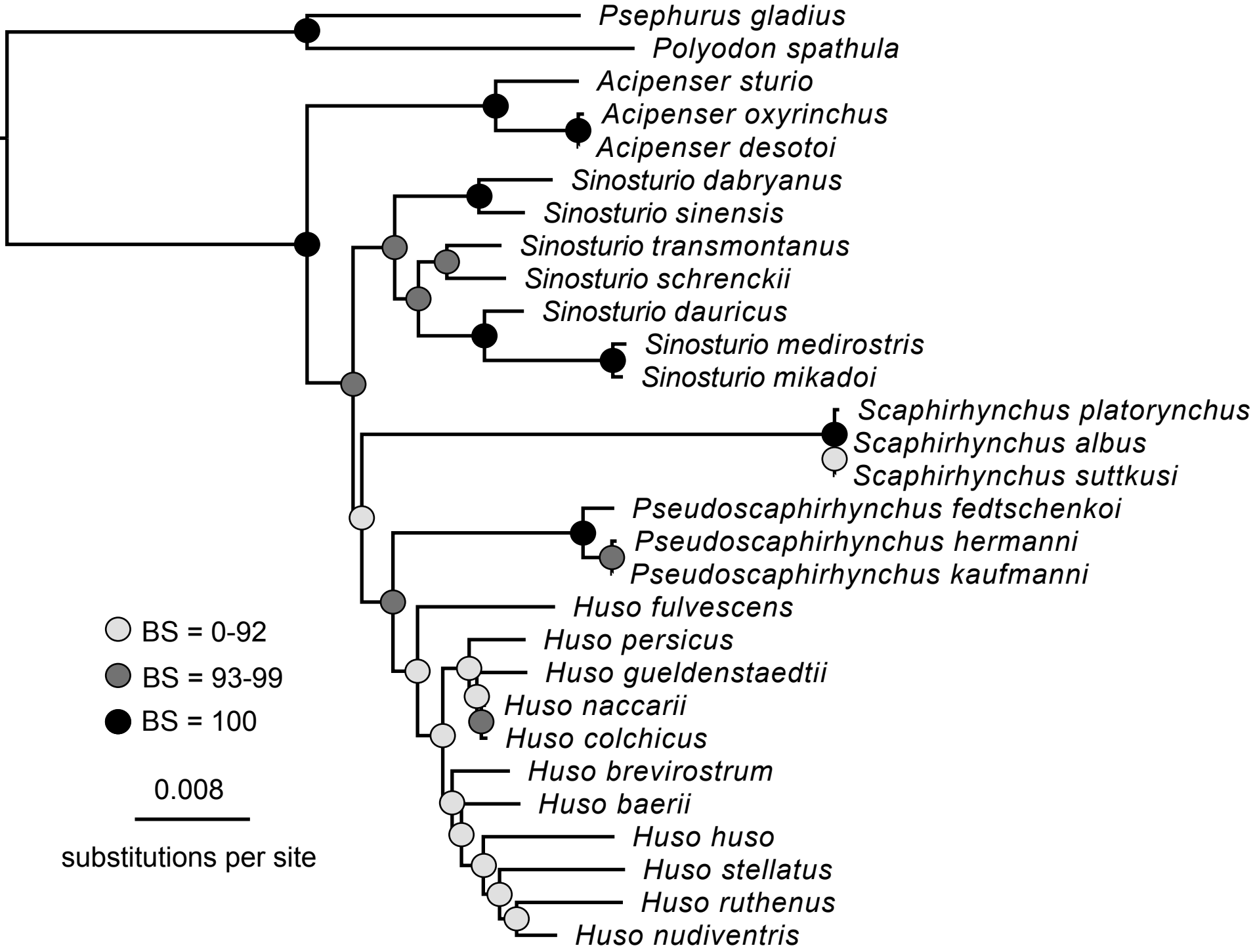
**Figure 3. Maximum Likelihood Phylogeny of Sturgeons Using Concatenated Nuclear and Mitochondrial DNA.** Maximum likelihood phylogeny generated in IQ-TREE 2 using concatenated sequences of 30 nuclear markers and *cytb* for 27 species of sturgeons and two species of paddlefishes. Numbers at nodes are ultrafast bootstrap supports.

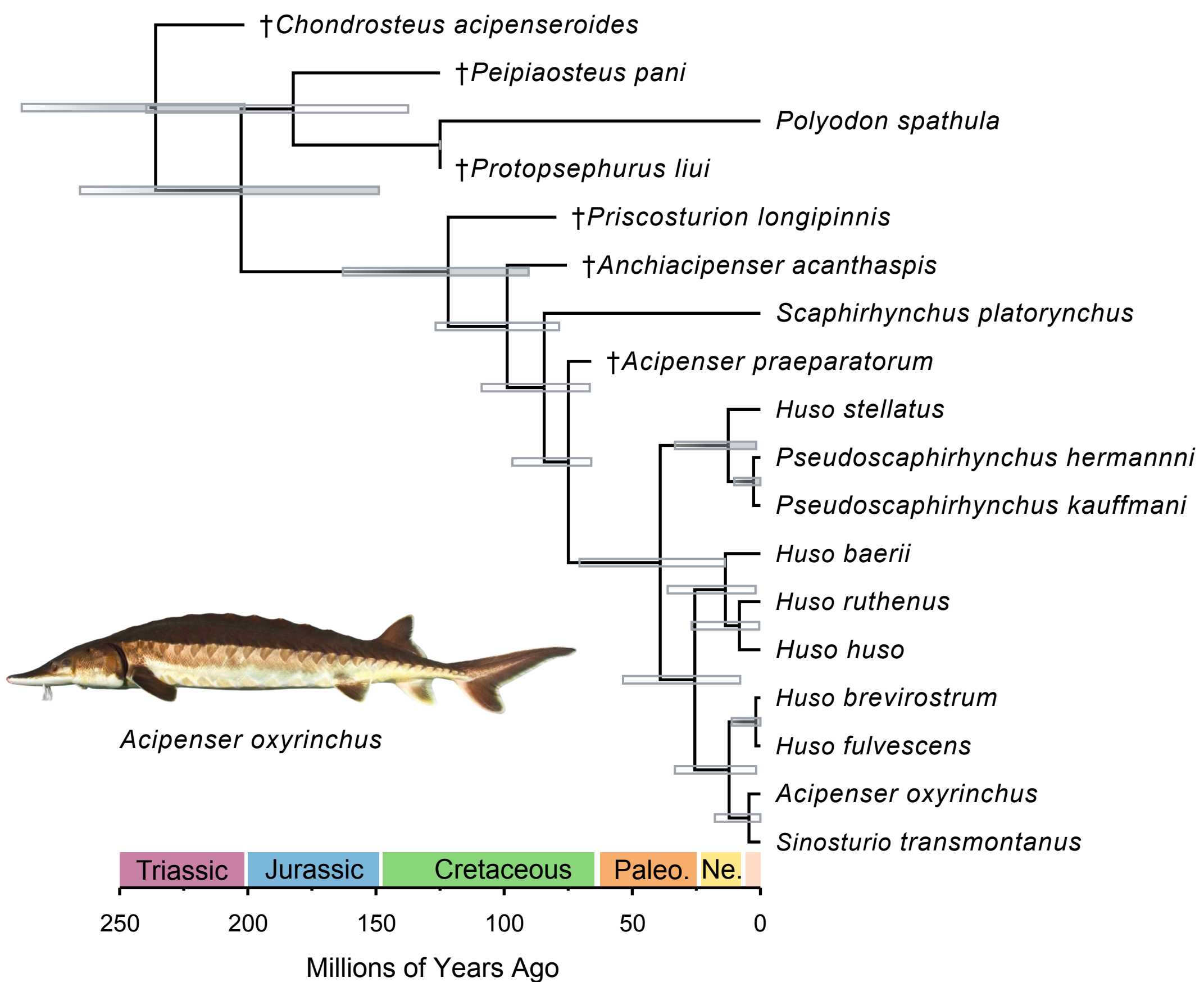
**Figure 4. Bayesian Tip-Dated Phylogeny of Sturgeons Using Morphological Data.** Time-calibrated maximum clade credibility tree with median node heights generated using 62 morphological characters coded for 18 living and extinct species of sturgeons and paddlefishes. Gray bars at nodes indicate 95% highest posterior density (HPD) intervals for divergence times, and clear bars indicate nodes with posterior support values less than 0.80. Abbreviations: Paleo. = Paleogene, N. = Neogene.

**Figure 5. Bayesian Tip-Dated Phylogeny of Sturgeons Using Molecular Data.** Time-calibrated maximum clade credibility tree with median node heights generated using the concatenated nuclear and mitochondrial DNA dataset for 27 species of sturgeons, two species of paddlefishes, and six fossil tip calibrations. Numbers at nodes are posterior support values. Gray bars at nodes indicate 95% highest posterior density (HPD) intervals for divergence times, and clear bars indicate nodes with posterior support values less than 0.80. Abbreviations: Paleo. = Paleogene, N. = Neogene.









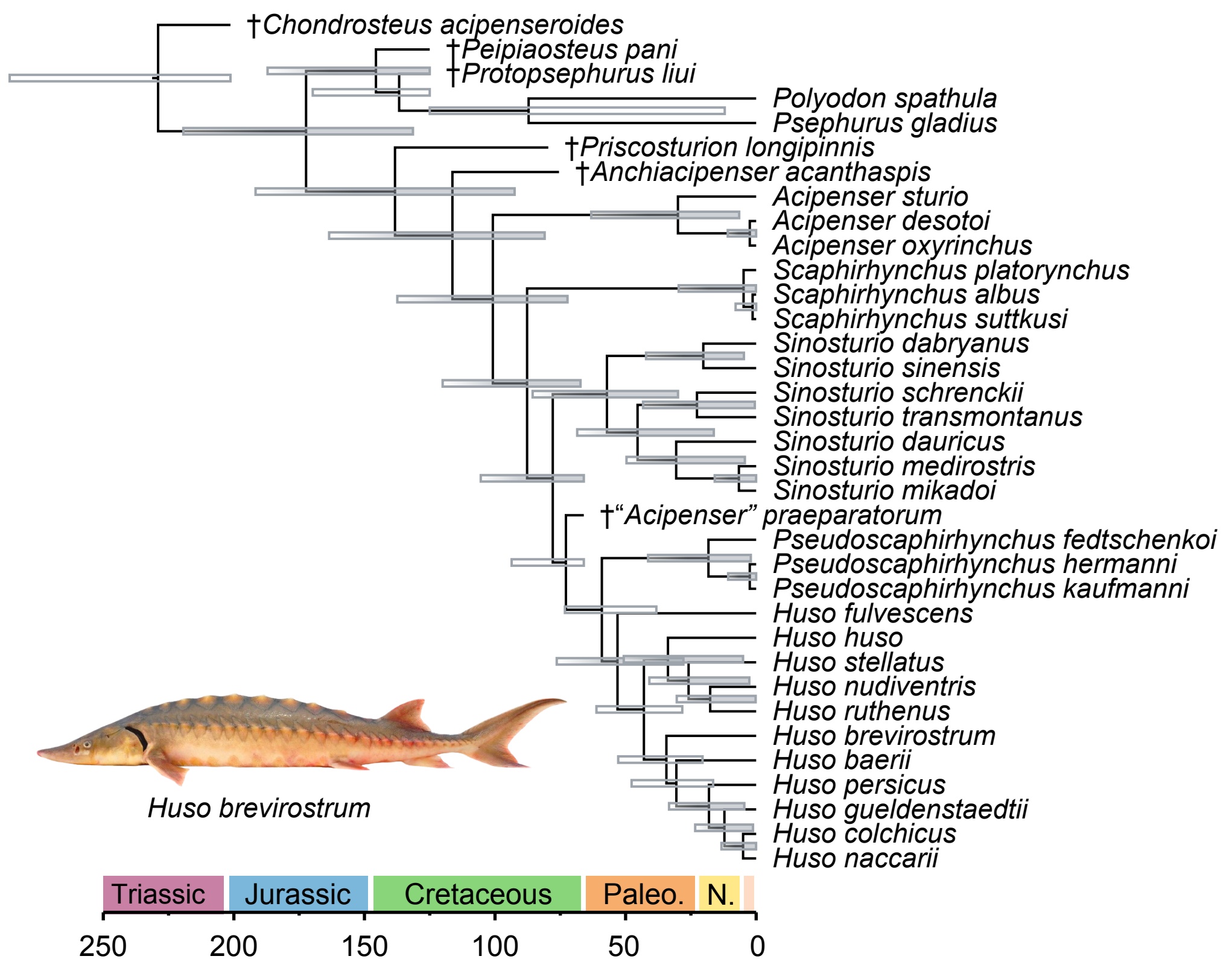


Table 1. Living species of *Acipenseridae* with common names and geographic distribution. Previous genus taxonomy provided for species with new genus species combinations.

Species	Common Name	Distribution	Previous Genus
<i>Acipenser desotoi</i>	Gulf Sturgeon	Gulf Coast of North America	
<i>Acipenser oxyrinchus</i>	Atlantic Sturgeon	Atlantic Coast of North America	
<i>Acipenser sturio</i>	European Sea Sturgeon	Atlantic Coast of Europe, Mediterranean, Aegean Sea, Black Sea	
<i>Huso baerii</i>	Siberian Sturgeon	Siberian Sea	<i>Acipenser</i>
<i>Huso brevirostrum</i>	Shortnose Sturgeon	Atlantic coastal rivers of North America	<i>Acipenser</i>
<i>Huso colchicus</i>	Caucasian Sturgeon	Black Sea	<i>Acipenser</i>
<i>Huso fulvescens</i>	Lake Sturgeon	Mississippi River system, Great Lakes, Hudson Bay	<i>Acipenser</i>
<i>Huso gueldenstaedtii</i>	Russian Sturgeon	Black Sea, Caspian Sea	<i>Acipenser</i>
<i>Huso huso</i>	Beluga	Adriatic Sea, Black Sea, Caspian Sea	
<i>Huso naccarii</i>	Adriatic Sturgeon	Adriatic Sea	<i>Acipenser</i>
<i>Huso nudiventris</i>	Ship Sturgeon	Black Sea, Caspian Sea, and Aral Sea	<i>Acipenser</i>
<i>Huso persicus</i>	Persian Sturgeon	Black Sea, Caspian Sea	<i>Acipenser</i>
<i>Huso ruthenus</i>	Sterlet	Azov Sea, Black Sea, Caspian Sea	<i>Acipenser</i>
<i>Huso stellatus</i>	Stellate Sturgeon	Azov Sea, Black Sea, Caspian Sea	<i>Acipenser</i>
<i>Pseudoscaphirhynchus fedtschenkoi</i>	Syr Darya Sturgeon	Syr Darya River in the Aral Sea Drainage	
<i>Pseudoscaphirhynchus hermanni</i>	Dwarf Sturgeon	Amu Darya River system in the Aral Sea Drainage	

<i>Pseudoscaphirhynchus kaufmanni</i>	Amu Darya Sturgeon	Amu Darya River system in the Aral Sea Drainage	
<i>Scaphirhynchus albus</i>	Pallid Sturgeon	Mississippi River system	
<i>Scaphirhynchus platyrhynchus</i>	Shovelnose Sturgeon	Mississippi River system	
<i>Scaphirhynchus suttkusi</i>	Alabama Sturgeon	Mobile Bay basin	
<i>Sinosturio dabryanus</i>	Dabry's Sturgeon	Yangtze River system, Yellow River system	<i>Acipenser</i>
<i>Sinosturio dauricus</i>	Kaluga	Amur River system	<i>Huso</i>
<i>Sinosturio medirostris</i>	Green Sturgeon	North Pacific Asia and North America	<i>Acipenser</i>
<i>Sinosturio mikadoi</i>	Sakhalin Sturgeon	North Pacific Asia, Bering Sea	<i>Acipenser</i>
<i>Sinosturio schrenckii</i>	Japanese Sturgeon	Amur River system	<i>Acipenser</i>
<i>Sinosturio sinensis</i>	Chinese Sturgeon	Yangtze River system, Pearl River system, Korean Peninsula, Japan	<i>Acipenser</i>
<i>Sinosturio transmontanus</i>	White Sturgeon	Pacific North America	<i>Acipenser</i>

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Table S1. Genbank Accession Numbers for *cytb* sequences analyzed in this study

Species	Genbank Accession
<i>Psephurus gladius</i>	AY571339
<i>Polyodon spathula</i>	NC004419
<i>Acipenser sturio</i>	NC027417
<i>Acipenser oxyrinchus</i>	KP997217
<i>Acipenser desotoi</i>	KP997218
<i>Sinosturio medirostris</i>	NC028405
<i>Sinosturio mikadoi</i>	KX276658
<i>Sinosturio dauricus</i>	NC023837
<i>Sinosturio dabryanus</i>	AY510085
<i>Sinosturio sinensis</i>	KJ174513
<i>Sinosturio transmontanus</i>	NC004743
<i>Sinosturio schrenckii SM</i>	MH973734
<i>Sinosturio schrenckii BG</i>	MH973733
<i>Huso naccarii</i>	MK078265
<i>Huso colchicus</i>	AF238695
<i>Huso gueldenstaedtii</i>	NC012576
<i>Huso persicus</i>	MW713795
<i>Huso baerii</i>	NC017603
<i>Huso brevirostrum</i>	MK078263
<i>Huso fulvescens</i>	NC030325
<i>Huso ruthenus</i>	KF153104
<i>Huso nudiventris</i>	NC030344
<i>Huso stellatus</i>	NC005795
<i>Pseudoscaphirhynchus fedtschenkoi</i>	NC058991
<i>Pseudoscaphirhynchus hermanni</i>	NC058992
<i>Pseudoscaphirhynchus kaufmanni</i>	NC050885
<i>Huso huso</i>	NC005252
<i>Scaphirhynchus albus</i>	NC030324
<i>Scaphirhynchus suttkusi</i>	NC036060
<i>Scaphirhynchus platorynchus</i>	NC030326

Table S2. Genbank Accession Numbers for nuclear gene sequences analyzed in this study

	<i>stx11a</i>	<i>cnr1</i>	<i>junbb</i>	<i>fam43a</i>	<i>flrt3</i>	<i>aplnra</i>	<b>LOC102693787</b>
<i>Huso baerii</i>	MH522337	MH522019	MH522161	MH522083	MH522113	MH521972	MH522193
<i>Sinosturio dabryanus</i>	MH522338	MH522020	MH522162	MH522084	MH522114	MH521973	MH522194
<i>Huso fulvescens</i>	MH522339	MH522021	MH522163	MH522085	MH522115	MH521974	MH522195
<i>Huso gueldenstaedtii</i>	MH522340	MH522022	MH522164	MH522086	MH522116	MH521975	MH522196
<i>Acipenser oxyrinchus</i>	MH522341	MH522023	MH522165	MH522087	MH522117	MH521976	MH522197
<i>Huso persicus</i>	MH522342	MH522024	MH522166	MH522088	MH522118	MH521977	MH522198
<i>Huso ruthenus</i>	MH522343	MH522025	MH522167	MH522089	MH522119	MH521978	MH522199
<i>Sinosturio schrenckii</i>	MH522344	MH522026	MH522168	MH522090	MH522120	MH521979	MH522200
<i>Sinosturio sinensis</i>	MH522345	MH522027	MH522169	MH522091	MH522121	MH521980	MH522201
<i>Huso stellatus</i>	MH522346	MH522028	MH522170	MH522092	MH522122	MH521981	MH522202
<i>Acipenser sturio</i>	MH522347	MH522029	MH522171	MH522093	MH522123	MH521982	MH522203
<i>Sinosturio transmontanus</i>	MH522348	MH522030	MH522172	MH522094	MH522124	MH521983	MH522204
<i>Sinosturio dauricus</i>	MH522349	MH522031	MH522173		MH522125	MH521984	MH522205
<i>Huso huso</i>	MH522350	MH522032	MH522174	MH522095	MH522126	MH521985	MH522206
<i>Pseudoscaphirhynchus kaufmanni</i>	MH522351	MH522033	MH522175		MH522127	MH521986	MH522207
<i>Polyodon spathula</i>	MH522352	MH522034	MH522176	MH522096	MH522128	MH521987	MH522208

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<i>Sinosturio dabryanus</i>	MH522290	MH522146	MH522210	MH522242	MH522354	MH522036
<i>Huso fulvescens</i>	MH522291	MH522147	MH522211	MH522243	MH522355	MH522037
<i>Huso gueldenstaedtii</i>	MH522292	MH522148	MH522212	MH522244	MH522356	MH522038
<i>Acipenser oxyrinchus</i>	MH522293	MH522149	MH522213	MH522245	MH522357	MH522039
<i>Huso persicus</i>	MH522294	MH522150	MH522214	MH522246	MH522358	MH522040
<i>Huso ruthenus</i>	MH522295	MH522151	MH522215	MH522247	MH522359	MH522041
<i>Sinosturio schrenckii</i>	MH522296	MH522152	MH522216	MH522248	MH522360	MH522042
<i>Sinosturio sinensis</i>	MH522297	MH522153	MH522217	MH522249	MH522361	MH522043
<i>Huso stellatus</i>	MH522298	MH522154	MH522218	MH522250	MH522362	MH522044
<i>Acipenser sturio</i>	MH522299	MH522155	MH522219	MH522251	MH522363	MH522045
<i>Sinosturio transmontanus</i>	MH522300	MH522156	MH522220	MH522252	MH522364	MH522046
<i>Sinosturio dauricus</i>	MH522301	MH522157	MH522221	MH522253	MH522365	MH522047
<i>Huso huso</i>	MH522302	MH522158	MH522222	MH522254	MH522366	MH522048
<i>Pseudoscaphirhynchus kaufmanni</i>	MH522303	MH522159	MH522223	MH522255	MH522367	MH522049
<i>Polyodon spathula</i>	MH522304	MH522160	MH522224	MH522256	MH522368	MH522050

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<i>Sinosturio dabryanus</i>	MH521989	MH522258	MH522306	MH522274	MH552933	MH552964
<i>Huso fulvescens</i>	MH521990	MH522259	MH522307	MH522275	MH552934	MH552965
<i>Huso gueldenstaedtii</i>	MH521991	MH522260	MH522308	MH522276	MH552935	MH552966
<i>Acipenser oxyrinchus</i>	MH521992	MH522261	MH522309	MH522277	MH552936	MH552967
<i>Huso persicus</i>	MH521993	MH522262	MH522310	MH522278	MH552937	MH552968
<i>Huso ruthenus</i>	MH521994	MH522263	MH522311	MH522279	MH552938	MH552969
<i>Sinosturio schrenckii</i>	MH521995	MH522264	MH522312	MH522280	MH552939	MH552970
<i>Sinosturio sinensis</i>	MH521996	MH522265	MH522313	MH522281	MH552940	MH552971
<i>Huso stellatus</i>	MH521997	MH522266	MH522314	MH522282	MH552941	MH552972
<i>Acipenser sturio</i>	MH521998	MH522267	MH522315	MH522283	MH552942	MH552973
<i>Sinosturio transmontanus</i>	MH521999	MH522268	MH522316	MH522284	MH552943	MH552974
<i>Sinosturio dauricus</i>	MH522000	MH522269	MH522317	MH522285	MH552944	MH552975
<i>Huso huso</i>	MH522001	MH522270	MH522318	MH522286	MH552945	MH552976
<i>Pseudoscaphirhynchus kaufmanni</i>	MH522002	MH522271	MH522319	MH522287	MH552946	MH552977
<i>Polyodon spathula</i>	MH522003	MH522272	MH522320	MH522288	MH552947	MH552978

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<i>Sinosturio dabryanus</i>	MH522226	MH522322	MH522068	MH522178	MH552949
<i>Huso fulvescens</i>	MH522227	MH522323	MH522069	MH522179	MH552950
<i>Huso gueldenstaedtii</i>	MH522228	MH522324	MH522070	MH522180	MH552951
<i>Acipenser oxyrinchus</i>	MH522229	MH522325	MH522071	MH522181	MH552952
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<i>Huso ruthenus</i>	MH522231	MH522327	MH522073	MH522183	MH552954
<i>Sinosturio schrenckii</i>	MH522232	MH522328	MH522074	MH522184	MH552955
<i>Sinosturio sinensis</i>	MH522233	MH522329	MH522075	MH522185	MH552956
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<i>Acipenser sturio</i>	MH522235	MH522331	MH522077	MH522187	MH552958
<i>Sinosturio transmontanus</i>	MH522236	MH522332	MH522078	MH522188	MH552959
<i>Sinosturio dauricus</i>	MH522237	MH522333	MH522079	MH522189	MH552960
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<i>Sinosturio dabryanus</i>	MH521957	MH522370	MH522098	MH522130	MH522005	MH522052
<i>Huso fulvescens</i>	MH521958	MH522371	MH522099	MH522131	MH522006	MH522053
<i>Huso gueldenstaedtii</i>	MH521959	MH522372	MH522100	MH522132	MH522007	MH522054
<i>Acipenser oxyrinchus</i>	MH521960	MH522373	MH522101	MH522133	MH522008	MH522055
<i>Huso persicus</i>	MH521961	MH522374	MH522102	MH522134	MH522009	MH522056
<i>Huso ruthenus</i>	MH521962	MH522375	MH522103	MH522135	MH522010	MH522057
<i>Sinosturio schrenckii</i>	MH521963	MH522376	MH522104	MH522136	MH522011	MH522058
<i>Sinosturio sinensis</i>	MH521964	MH522377	MH522105	MH522137	MH522012	MH522059
<i>Huso stellatus</i>	MH521965	MH522378	MH522106	MH522138	MH522013	MH522060
<i>Acipenser sturio</i>	MH521966	MH522379	MH522107	MH522139	MH522014	MH522061
<i>Sinosturio transmontanus</i>	MH521967	MH522380	MH522108	MH522140	MH522015	MH522062
<i>Sinosturio dauricus</i>	MH521968	MH522381	MH522109	MH522141	MH522016	MH522063
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<i>Pseudoscaphirhynchus kaufmanni</i>	MH521970	MH522383	MH522111	MH522143		MH522065
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