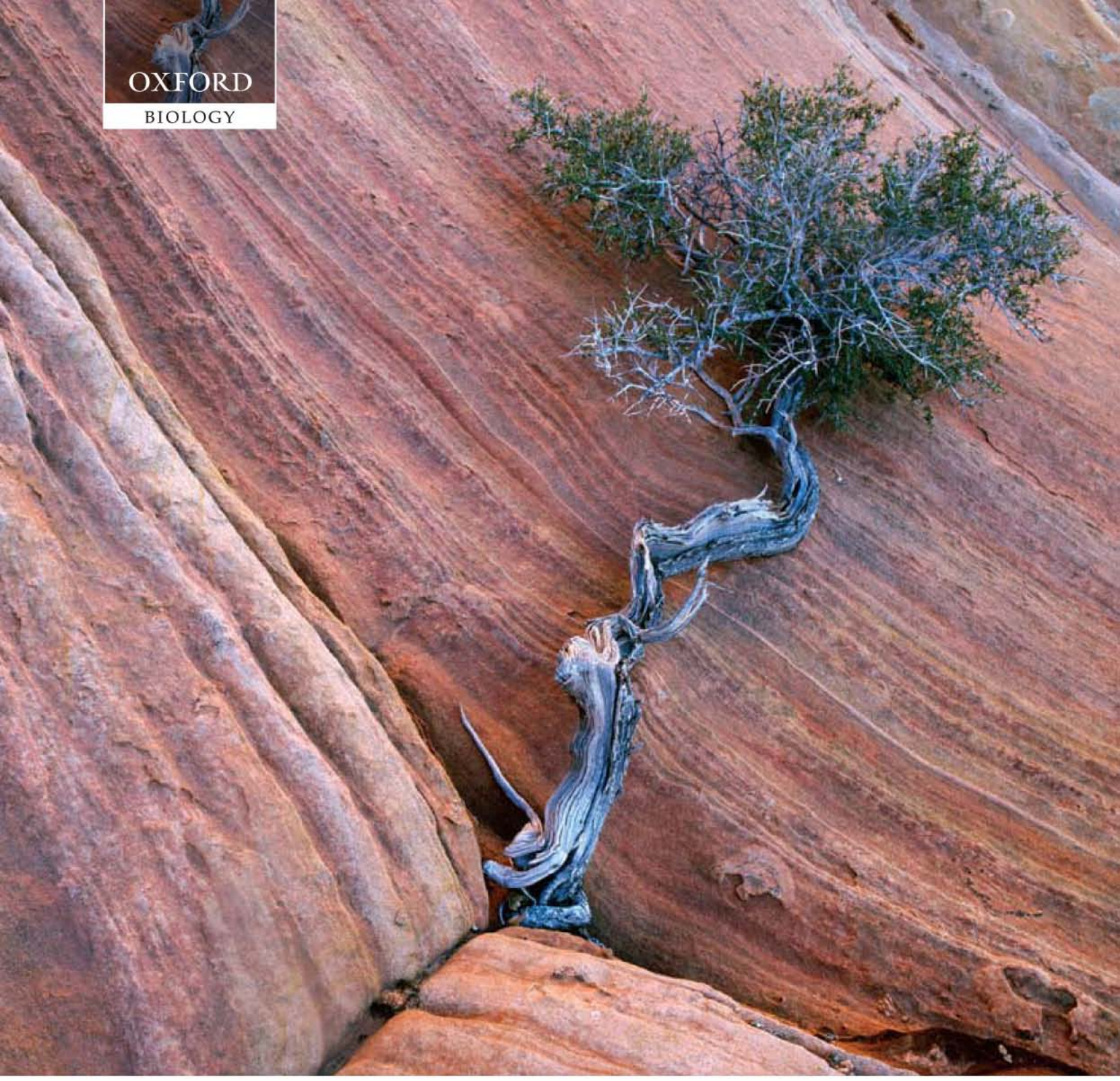

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Sturgeons and paddlefishes (Acipenseriformes)

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Abstract

The Order Acipenseriformes includes 25 living sturgeon species and two living paddlefish species, which are commonly considered "living fossils." Phylogenetic analyses have supported two morphological divisions within acipenseriforms, Polyodontidae (paddlefishes) and Acipenseridae (sturgeons). Divergence times from molecular data range from 184 million years ago (Ma) to 114 Ma, although the oldest time is considered to be the most reliable and is in better agreement with the fossil record. The molecular estimates and fossil record suggest that the major lineages of Acipenseriformes diversified in the Jurassic and early Cretaceous (~180–100 Ma), probably associated with continental breakup.

The extant sturgeons (Acipenseridae, containing four genera—*Acipenser*, *Huso*, *Pseudoscaphirhynchus*, and *Scaphirhynchus*) and paddlefishes (Polyodontidae, containing two monospecific genera—*Polyodon* and *Psephurus*) with some extinct families form a monophyletic group of the ray-finned fishes, the Order Acipenseriformes. Sturgeons are diagnosed by presenting five rows of bony scutes or plates on their body, four barbels in front of mouth, and absence of teeth in adults. Paddlefishes are diagnosed by their paddle-like snout, absence of large scutes on their body, and minute barbels on their snout (*1*). Additionally, *Polyodon* is best known for its filtered-feeding habit based on numerous thin, elongate gill rakers unique to them among sturgeons and paddlefishes (*2*).

Acipenseriforms only inhabit the Northern Hemisphere, and the present biogeographic distribution of the extant species of this group reflects ancient relationships among fish faunas of Europe, Asia, and North America. Extant representatives are in two families with six genera and 27 species. Here, we review the relationships and divergence times of the major groups of acipenseriforms (Fig. 1).

Until recently, our knowledge of the phylogenetic relationships of sturgeons and paddlefishes was mainly based on anatomical studies (*3, 4*). Researchers usually agree that the diversification of the living acipenseriforms may go back to the Jurassic, where sturgeons and paddlefishes were already diversified (*5*).

The first comprehensive study (*6*) using molecular data, partial sequences of the mitochondrial genes *cytochrome b* (*cyt b*), *16S rRNA*, and *12S rRNA*, drew three major conclusions: the Pallid Sturgeon, *Scaphirhynchus albus*, was suggested as the closest species to all species of *Acipenser* and *Huso*; the two *Huso* species were embedded within *Acipenser*; and three major clades were proposed. Those clades were *Acipenser sturio–Acipenser oxyrinchus*, *Acipenser schrenckii–Acipenser transmontanus*, and all Ponto-Caspian species plus *Acipenser dabryanus* and *Acipenser brevirostrium*. However, these conclusions were tentative due to both limited taxa sampling as well as use of relatively short, partly nondiagnostic, gene fragments.

More recently, studies using combined DNA data sets (4012 bp) from five (*7*) mitochondrial genes (*cyt b*, *12S rRNA*, *cytochrome c oxidase subunit II*, $tRNA_{Asp}$, and $tRNA_{Phe}$) and two (*8*) mitochondrial gene regions (*16S rRNA* and *NADH5*) and comprehensive taxonomic coverage resulted in five well-supported conclusions: (i) the two species of paddlefish form a monophyletic clade;

Fig. 1 A juvenile Shortnose Sturgeon from North America, *Acipenser brevirostrum*. Credit: M. H. Sabaj.

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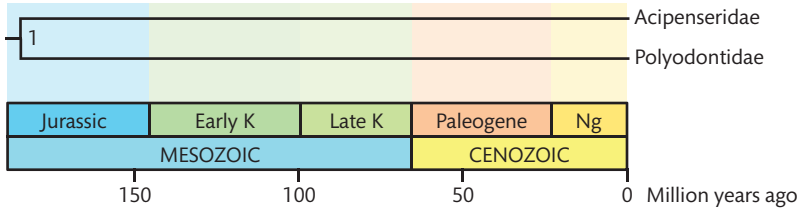

Fig. 2 A timetree of sturgeons and paddlefishes (Acipenseriformes). Divergence times are shown in Table 1. *Abbreviations*: Ng (Neogene) and K (Cretaceous).

(ii) *Acipenser* and *Scaphirhynchus* form a monophyletic assemblage, the Acipenseridae, the most basal position within them remains unresolved, held either by the genus *Scaphirhynchus* or by the clade containing the sea sturgeons (*A. oxyrinchus* and *A. sturio*); (iii) the two species of *Huso* are embedded within the genus *Acipenser*; (iv) there are two monophyletic groups within the *Acipenser*/*Huso* assemblage closely correlated to their geographic distribution—the Atlantic clade and the Pacific clade; and (v) the three species of *Pseudoscaphirhynchus* are clustered within the Atlantic clade of *Acipenser*/*Huso* (*7, 9, 10*).

Only one study has estimated divergence times among major groups of acipenseriforms in a comprehensive manner so far. Based on complete mitochondrial genome data and using the Bayesian relaxed molecular clock method (*10*), the estimated origin time for Acipenseriformes was at 390 million years ago (Ma) with a 95% credibility interval of 414–362 Ma, and the estimated time for splitting between sturgeons and paddlefishes was at 141 Ma with a 95% credibility interval of 160–132 Ma (Table 1). This latter time estimate was similar to estimates from two data sets presented in another study, 114 Ma and 145 Ma (*11*). Using more taxa but only one gene (*cyt b*), the estimate for the sturgeon–paddlefish split was somewhat older, 184 Ma (*10*).

The divergence time of the two families shown in the timetree (Fig. 2), 184 Ma, reflects the recent estimate based on *cyt b*, which is in better agreement with the fossil record (*10*). Together with a more detailed timetree of species relationships based on *cyt b* (*10*), and the fossil record, this suggests that most of the major splits in Acipenseriformes occurred during the Jurassic and early Cretaceous, ~180–100 million years ago. These splits were most probably related to the continental breakup. Within the Polyodontidae clade the Chinese Swordfish (*Pseudoscaphirhynchus gladius*), with a limited distribution in Yangtze River, splits with the Mississippi Paddlefish (*Pseudoscaphirhynchus spathula*), which also has a limited distribution in the Mississippi–Missouri basin, at ~68 Ma. Within the Acipenseridae, the divergence time between the *A. oxyrinchus–A. sturio* cluster and the rest of the acipenserids appears as ~172 Ma; the divergence time between *Scaphirhynchus* and the *Acipenser*/*Huso* assemblage appears as about 151 Ma; the divergence time between the Pacific and the Atlantic clades appears as about 121 Ma (*10*).

Acipenseriformes has existed at least since the early Jurassic (~200 Ma), and all fossil and recent taxa are from the Holarctic biogeographic region (*2*). The Atlantic and Pacific Oceans seemingly began to open during the Jurassic and have continued opening during the Cretaceous. About 120 million years ago, the Tethys Sea shrank further, eventually becoming the Black, Caspian, and Aral Seas (*12*). These geological events appear to have played an important role in acipenseriform diversification and evolution (*6, 10*). In summary, the acipenseriform timetree shows Jurassic to mid-Cretaceous diversification of sturgeons and paddlefishes, which is indirectly supported by fossil evidence (*3, 4, 13*) and is consistent with continental movements and paleogeography.

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Table 1. Divergence time estimates (Ma) and their confidence/credibility intervals (CI) between sturgeons and paddlefishes (Acipenseriformes).

Timetree		Estimates			
Node	Time	Ref. (*10*)(a)		Ref. (*10*)(b)	
		Time	CI	Time	CI
1	184	184	200–150	141	160–132

Note: The estimates are from a Bayesian relaxed clock analysis of two data sets: (a) *cytochrome b* gene (b) complete mitochondrial genome data. The node time in the timetree uses estimate (a).

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