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E. O. WILEY

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# The Phylogeny and Biogeography of Fossil and Recent Gars (Actinopterygii: Lepisosteidae)

BY

E. O. WILEY

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## Abstract

The relationships, taxonomy, and biogeography of gars are the focus of this study. The phylogenetic method of Hennig (1966) is used to analyze current hypotheses concerning the relationships among gars and of gars to other actinopterygian groups. Hennig's method is discussed and several points taken up in detail. Croizat's (1958) method of biogeographic analysis is used to describe the major features of gar biogeography.

Gars comprise a monophyletic group, the sister-group of the Halecostomi (Amiidae plus Teleostei). These three taxa comprise another monophyletic group, the Neopterygii, the sister-group of the Chondrostei. These conclusions corroborate certain previous hypotheses and refute others.

Sixteen species of gars are recognized. They are split equally among two genera, *Lepisosteus* and *Atractosteus*. The genus *Lepisosteus* includes a newly described fossil species from the Cretaceous of Montana and the following seven species in approximate phylogenetic order: *L. cuneatus* (Eocene, North America); *L. platostomus* (Recent, North America); *L. indicus* (Cretaceous, India); *L. osseus* (Recent, North America); *L. fimbriatus* (Eocene and Oligocene, Europe); *L. oculatus* (Recent, North America); *L. platyrhincus* (Recent, North America). The interrelationships of these species are discussed.

The genus *Atractosteus* includes, in approximate phylogenetic order: *A. strausi* (Eocene, Europe); *A. tropicus* (Recent, Middle America); *A. simplex* (Eocene, North America); *A. africanus* (Cretaceous, Africa); *A. occidentalis* (Cretaceous, North America); *A. atrox* (Eocene, North America); *A. spatula* (Recent, North and Middle America); and *A. tristoechus* (Recent, Cuba and the Isle of Pines).

Track analysis of the biogeographic distributions of both genera indicate that both may have had a Pangean distribution and the minimum age for both genera is hypothesized to be 180 million years before present. Various tracks within each genus are discussed and relative levels of vicariance are hypothesized.


## Introduction

The lepisosteids, or gars, are carnivorous fishes of sluggish habits and are now restricted to the Western Hemisphere from Costa Rica to southern Canada. Fossil gars are known from North America (Cretaceous to Recent), Europe (Cretaceous to Oligocene), Africa (Cretaceous), and India (Cretaceous). There are seven currently recognized Recent species (Suttkus, 1963) and nine diagnosable fossil species.

The living gars inhabit the larger rivers, streams, and lakes of their range. Some species also frequent brackish and marine coastal waters (see Suttkus, 1963, for a summary of occurrence in these habitats). Anatomically, they combine various primitive (plesiomorphous) and derived (apomorphous) characters. Notably primitive characters include interlocking ganoid scales, skull roofing bones with enameloid tubercles, a semi-heterocercal tail, and fulcral scales on the medial fins (Suttkus, 1963; Patterson, 1973). Derived characters not found in any other group of actinopterygians include an attenuated snout produced by ethmoid elongation, opisthocoelous vertebrae, and plicidentine teeth.

The structure and development of gars have been extensively studied since the first works of Louis Agassiz (1834, 1843; anatomy) and Alexander Agassiz (1878; general aspects of early development). These studies include:

Early development: Wright, 1879; Balfour and Parker, 1882 (many aspects of both development and structure, comparisons with other fishes); Beard, 1889; Mark, 1890; Dean, 1895a, 1895b, 1896a, 1896b (comparisons with *Amia*); Ziegler, 1900; Reighard and Phelps, 1908 (adhesive organ); Lindahl, 1944 (adhesive organ and hypophysis); and Virchow, 1894.

Skull development: Parker, 1882; Veit, 1907, 1911, 1924 (chondrocranium); Hammarberg, 1937 (chondrocranium and dermal bones); Aumonier, 1941 (dermal bones).

Vertebrae and ribs: Gegenbaur, 1867; Baur, 1887 (ribs); Schaeffer, 1967a (vertebrae).

Miscellaneous developmental studies: Wilder, 1876, 1877 (fins and brain); Nickerson, 1893 (scales); Beard, 1895 (pronephrons), 1896 (yolk sac and merocytes); Allen, 1911 (origin of sex cells); Landarce and Conger, 1913 (lateral line primordia); Brookover, 1914 (olfactory nerve); Hammett and Hammett, 1939 (proportional snout length); Garrett, 1942 (corpuscles of Stannius); Kullin, 1950 (forebrain); Bodemer, 1957 (extrinsic ocular muscles); Kerr, 1967 (teeth); Jessen, 1972 (pectoral girdle).

Skull structure: Veit, loc. cit.; Baur, 1889a (comparison of occipital region with *Amia*); Allis, 1919 (comparison of otic region with other fishes); De Beer, 1926 (comparison of orbito-temporal region with other fishes); Rayner, 1948 (neurocranial ossifications compared to other fishes); Patterson, 1973 (comparisons with other neopterygians), 1975 (comparison with other actinopterygians); Reagan, 1923 (skeleton, with comparisons); Mayhew, 1924 (skull ossifications); Gregory, 1933 (comparisons with other fishes); Holmgreen and Stensiö, 1936 (skull and visceral arches); Westoll, 1937 (cheek bones); Stensiö, 1947 (relationship of lateral line system to skull bones); Parrington, 1956 (patterns of dermal bone ossification); Gosline, 1965 (circumorbital bones); Gardiner 1963 (snout), 1967 (preopercular).

Sensory canals: Collinge, 1892, 1895; Allis, 1905, 1934; Stensiö, loc. cit.

Hyoid arch: Tatarke, 1939; Bertmar, 1967; McAllister, 1968; Nelson, 1969a.

Visceral skeleton: Wijhe, 1880, 1882; Allis, 1911; Edgeworth, 1911, 1935 (muscles); Holmgren and Stensiö, loc. cit.; Nelson, 1969a.

Pectoral girdle: Sewertzoff, 1934; Querternous, 1967 (cleithral shape); Jessen, 1972, 1973 (with comments on course of spinal nerves in vertebral region).

Vertebrae and ribs: Baur, 1887, 1889b; Haines, 1942; Schaeffer, 1967a.

Scale morphology: Agassiz, 1843; Williamson, 1849, 1851; Jackson, 1856, Reissner, 1859; Nickerson, 1893; Scupin, 1896; Goodrich, 1909; Kurr, 1952; Suttkus, 1963.

Swimbladder: Valentine, 1840; Hoeven, 1841; Hyrtl, 1852a; Parkard, 1859.

Respiratory function of the swimbladder: Weidersheim, 1904; Potter, 1927; Suttkus, 1963; McCormack, 1967; Renfo and Hill, 1970; Rahn, Rahn, Howell, Gans, and Tenney, 1971; Hill, Schnell, and Echelle, 1973.

Other anatomical studies include: Wyman, 1844 (tooth structure); Müller, 1844 (gut); Wilder, 1877 (brain), 1878, (gut); Hyrtl, 1851, 1852b (arteries); Macallum, 1886 (gut and pancreas); Kingsbury, 1897 (encephalic invaginations); Müller, 1897 (pseudobranchs); Allis, 1908 (pseudobranchs); Allen, 1907, 1908 (subcutaneous blood vessels of the head and tail respectively); Brookover, 1908 (Pinkus's nerve); Theunissen, 1914 (motor nerve arrangement); Danforth, 1916 (coronary and hepatic nerves); Casto, 1966 (liver); Landolt and Hill, 1975 (gill area and respiration). Finally, Goodrich (1930) and Jollie (1962) provide good summary information on gar anatomy.

Although traditionally considered primitive actinopterygian fishes, the relationships of gars to other major groups have been controversial. Various authors aligned them with the polypterids (Müller, 1844), the amiids (Huxley, 1861; Goodrich, 1909, 1930; Berg, 1940, 1965; Rayner, 1941, 1948; Nelson, 1969a; Jessen, 1972, 1973, and others), and a group composed of amiids and teleosts among Recent fishes (Westoll, 1944; Gardiner, 1960, 1963, 1967; Patterson, 1973). Among fossil forms, gars have been aligned with aspidorhynchids (Reis, 1887), or semionotids (Rayner, 1941, 1948; Gardiner, 1963, 1967; Romer, 1966), or have been set apart from other known fossil groups (Patterson, 1973). Regardless of the alignment proposed, no author