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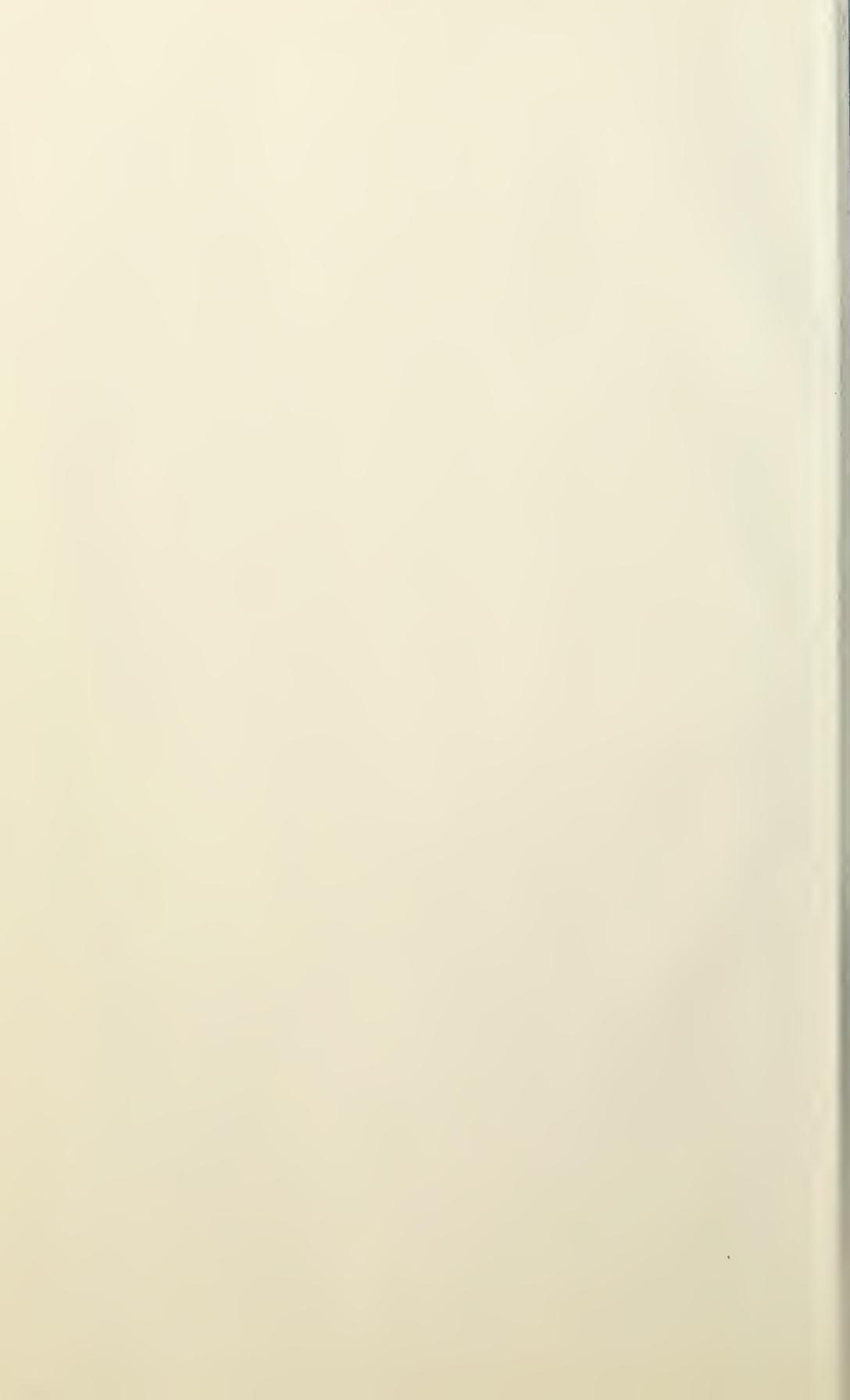


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**The Phylogeny and Biogeography  
of Fossil and Recent Gars  
(Actinopterygii: Lepisosteidae)**

By  
**E. O. Wiley**

UNIVERSITY OF KANSAS  
LAWRENCE 1976

November 12, 1976

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

BY

E. O. WILEY

*A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York, 1976.*

THE UNIVERSITY OF KANSAS  
LAWRENCE  
1976

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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 Amer-

ica); *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. trausi* (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, opisthocoealous 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 (skull, with comparisons); Mayhew, 1924 (skull ossifications); Gregory, 1933 (comparisons with other fishes); Holmgren 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; Quertermus, 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; Suttikus, 1963.

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

Respiratory function of the swimbladder: Weidersheim, 1904; Potter, 1927; Suttikus, 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

has doubted their monophyly and gars usually are put in an order or division of their own (Ginglymodi of Cope, 1872; Patterson, 1973; Lepidosteiformes of Berg, 1940; Lepisosteoi of Suttkus, 1963). The name Ginglymodi is used here for reasons of priority.

One of the major aims of this study is to evaluate the various hypotheses of ginglymod relationships to other actinopterygian groups using the phylogenetic methodology of Hennig (1966). Various characters of the skull, hyoid and visceral arches, pectoral girdle, and axial skeleton of gars are compared to chondrosteans, semionotids, halecomorphs (*Amia*, etc.), and teleosts. Analyses of characters are extended to other groups where needed. Characters not previously hypothesized as plesiomorphous or apomorphous are interpreted while characters previously interpreted as plesiomorphous or apomorphous (for example, those studied by Nelson, 1969a, and Patterson, 1973) are re-evaluated. Particular attention is placed on synapomorphies which corroborate the monophyletic nature of the Ginglymodi and the synapomorphic characters shared among groups of actinopterygians which indicate ginglymod relationships.

Recent gars are a relatively well known component of the North and Middle American fish fauna. Except for the work of Suttkus (1963), there has been little recent systematic work on the group, and no comprehensive study of their interrelationships. Gar nomenclature began with Linnaeus' (1758) description of *Lepisosteus osseus*, which he placed with the pikes in the genus *Esox*. Bloch and Schneider (1801) followed Linnaeus' generic placement when they described *Atractosteus tristoechus*. Lacépède (1803) placed the gars in their own genus, *Lepisosteus*. Rafinesque (1818a, 1818b, 1820) added four genera, *Litholepis* (a mythical fish drawn by Audubon), *Sarchirus*, *Cylindrosteus*, and *Atractosteus*. Cuvier (1825) erected the family Lepisosteidae. Throughout the

nineteenth century many nominal Recent species were described by such workers as Agassiz (1843), De Kay (1842), Girard (1858), Gill (1863), Winchell (1864), and Duméril (1870). The majority of these names since have been placed in synonymy. The proliferation of synonyms was brought about primarily by misunderstanding of ontogenetic changes and geographic variation, and a tendency on the part of some workers to describe specimens from newly sampled areas as new species.

The nomenclature and relationships of Recent gars was in confusion throughout the nineteenth century and the first part of the twentieth century because of a poor understanding of the nominal genera and the large number of synonyms thought valid. Agassiz (1848) divided gars into sharp-nosed and flat-nosed species and (1850) commented on the species he thought valid. Cope (1865) and Fowler (1910) recognized two genera, *Lepisosteus* and *Cylindrosteus*. Duméril (1870) recognized these genera plus *Atractosteus*. Jordan and his colleagues attempted to deal with the nomenclature of the entire family, while accepting the many genera and species then current (Jordan, 1885; Jordan and Gilbert, 1883; Jordan and Evermann, 1896; Jordan, Evermann, and Clark, 1930). All these efforts to comprehend gar relationships resulted in a complicated nomenclature, since simplified by recognition of a single genus, *Lepisosteus* (Hubbs and Lagler, 1943; Eddy, 1957; Moore, 1957, 1968; Suttkus, 1963), and seven recent species (Suttkus, 1963). Suttkus (1963) provided a key to these species, re-described four of them, and split the genus into two subgenera, *Lepisosteus* and *Atractosteus*. For reasons discussed below, I recognize these subgenera as genera.

The genus *Atractosteus*, as defined here, includes three extant named species; *A. spatula* Lacépède (North and Middle America), *A. tristoechus* (Bloch and Schneider) (Cuba and the Isle of

Pines), and *A. tropicus* Gill (Middle America). In addition, there is a still undescribed narrow-snouted morphotype from the coastal plain of Texas. The status of this morphotype cannot be decided until more material is available for study.

The genus *Lepisosteus*, as defined here, includes four living species, *L. platostomus* (Rafinesque), *L. osseus* (Linnaeus), *L. oculatus* Winchell, and *L. platyrhincus* (DeKay), all found in the eastern half of North America.

Fossil gars are found in North America, Europe, Africa, and India. Most names are based on fragmentary material and the number of valid morphotypes and their interrelationships are essentially unknown. Nevertheless, as discussed below, all of the fossil material can be assigned to one or the other Recent genus.

Wood (1846) described the first fossil gar, *Lepisosteus fimbriatus*, a European species from the Eocene and Oligocene commonly known as *L. suessionensis* Gervais (1853). Leidy described three of the five North American species recognized here; *A. occidentalis* (Leidy, 1856a; Cretaceous), *A. atrox* (Leidy, 1873a, Eocene), and *A. simplex* (Leidy, 1873a, Eocene). The specimens Leidy used for his descriptions were undiagnosable, but later workers (Eastman, 1900a; Estes, 1964) described these morphotypes and associated the names with more complete and diagnostic material. Cope (1884) described the fourth recognized morphotype from the North American Eocene, *L. cuneatus*. He placed this morphotype in the genus *Clastes*. These and other workers also named a number of forms not considered valid here. The last North American morphotype recognized here, *L. opertus*, is described as a new species from the Cretaceous. Kinkelin (1884) added the second European species recognized here, *A. strausi*. Woodward (1908) described *L. indicus* from the Cretaceous of India. The last form rec-

ognized here is *A. africanus*, described by Arambourg and Joleaud (1943) under the generic name *Paralepidosteus*.

Two workers, Woodward (1895) and Hay (1902, 1929), attempted to deal with fossil gars as a group. Woodward (1895) justifiably doubted the validity of many of the described forms. Hay (1902, 1929) summarized the literature on North American fossil gars.

The species listed above are treated in a formal systematic account. This is organized according to the phylogenetic relationships among the species. The division, family and genera are diagnosed by synapomorphies (shared derived characters). Each species is placed in phylogenetic order within its respective genus by a listing convention that was previously discussed by Nelson (1972a) and applied to neopterygian fishes by Patterson and Rosen (in press). The species are diagnosed and synonymies provided. The synonymies of Recent species include only name changes or significant systematic references, whereas those of fossil forms include all references found. Fossil material not diagnosable to species is listed by its assigned name at the level at which its affinities can be assessed (for example, *Atractosteus* sp. indet., *incertae sedis* *Atractosteus africanus*, etc.). The objective of the systematic accounts is to elucidate relationships among species and not to evaluate intraspecific variation. Thus, the descriptive comments are largely confined to characters important for relationships of named taxa and only secondarily to intraspecific variation that might cause problems in identification of those taxa.

In the analysis of phylogenetic relationships among gars, each character is analyzed to determine its relative apomorphic (derived) or plesiomorphic (primitive) nature. After character analysis, the relationships among taxa are summarized in a series of phylogenetic hypotheses for each genus.

There have been few discussions of

gar biogeography outside of descriptions of ranges. Casier (1961) discussed the biogeography of fossil gars. Rosen (1975) has discussed the distribution of *Atractosteus* in relation to generalized features of the Middle American and Antillean biotas. Rosen's discussion followed a "vicariance" methodology proposed by Croizat (1958, 1962) and summarized by Croizat, Nelson, and Rosen (1974). His views are evaluated in light of current knowledge of gar relationships. Distribution of the other Recent and fossil species are also analyzed by the same "vicariance" methodology.

The purposes of this study, stated above, can be summarized in a series of questions:

1. Are the gars a monophyletic group? If so, what characters do they exhibit that corroborate this hypothesis?
2. What characters shared by gars with other actinopterygians permit the evaluation of various hypotheses of actinopterygian relationships? Which hypothesis is to be preferred?
3. What Recent and fossil species can be recognized within the Family Lepisosteidae? What are the relationships among these species as evidenced by shared derived (synapomorphous) characters?
4. What are the distributional patterns of the family and the monophyletic groups within the family? Can these patterns be tied to generalized patterns of distribution reported by other workers?

#### MATERIALS AND METHODS

Fossil and Recent specimens from a number of institutions were used. The material examined is listed for each species in the systematic account by State or Country and District, and locality (if a fossil) in Appendix A, Material Examined. Catalogue Numbers of important specimens of other actinopterygian groups are referred to in the text. Structural abbreviations used in figures are identified in the figure caption. Institu-

tional abbreviations are defined in Appendix A.

*Fossil preparations.*—Fossil preparations include acid, mechanical, and lye preparations. The lye technique was apparently originated by Herr Otto Feist of Neider-Ramstadt, West Germany who uses the technique for preparing specimens from the Messel formation, including the specimens of *Atractosteus trausti* described here. Herr Feist imbeds the specimens in fiberglass (apparently in the field), soaks them in a lye solution and scrubs them with brushes, beginning with wire and ending with a toothbrush. I have used a strong KOH solution with the same results. Specimens need little additional preparation. The lye apparently breaks down the hydrocarbons in the Messel matrix, which is a kind of compressed peat.

*Recent preparations.*—Recent specimens examined included articulated and disarticulated Recent osteological material, alizarin preparations, and alcohol preserved whole material. Gill arch structure was studied in alcohol preserved specimens by excising the arch, soaking it in distilled water overnight, staining it with Alizarin red S, destaining in distilled water, and returning it to alcohol (this procedure from G. Nelson, pers. comm.). Muscle, bone, and cartilage patterns were determined by visual inspection. Cartilage was stained with Methylene blue and destained in alcohol during inspection.

*General methods.*—Osteological and myological patterns and meristic counts were determined by visual inspection with and without optical aids. Bausch and Lomb and Wild dissecting microscopes were used. Meristic counts follow those of Suttikus (1963). Enameloid patterns were determined by visual inspection of unprepared bone and checked in representative specimens of each species by either staining the bone with alizarin (which does not stain the enameloid) or by "smoking" the bone with ammonium chloride (which brings out the enam-

eloid and bony ridges in relief). The ammonium chloride technique was used for bone photography. Drawings were made with the use of several optical devices, including the camera lucida, copy stand, and tracing from photographs. Approximate dimensions of drawings or photographs are provided by a 10 mm bar below the figure or by stating the greatest length of the figured specimen.

Color patterns were determined by visual inspection of preserved specimens. The following terms are used to describe these color patterns:

**Blotch:** a concentration of melano-phores forming a large pigment patch with more or less definite borders.

**Flank stripe:** a pigment stripe running anteriorly along the side from the base of the caudal fin to or through the eye.

**Dorsal stripe:** a pigment stripe running anteriorly along the dorsum from the base of the caudal fin to the nape of the head.

**Belly stripe:** a pigment stripe running posteriorly from the base of the pectoral fin to the base of the anal fin along the lateral edge of the belly on each side of the midline. Belly stripes on each side usually join at the anal fin base to continue posteriorly as a medial ventral stripe on the caudal peduncle.

**Preopercular stripe:** a pigment stripe running along the lateral arm of the preopercular from its junction with the subopercular anteriorly to the lower jaw.

**Retroarticular stripe:** a small vertical pigment stripe on the back of the lower jaw.

**Lower jaw stripe:** usually a continuation of the flank stripe on the lower jaw, and occasionally a separate pigment stripe on the coronoid process.

Measurements were taken with either a dial micrometer or dividers measured against a metric rule. Reported measurements were selected because they were obtainable or partly obtainable from some fossil, as well as Recent specimens. Neither the measurements nor counts

presented here are meant to represent statistical samples, nor to characterize adequately the variation expected in Recent North American species. Dr. Royal Suttkus (Tulane University) has taken and continues to take extensive meristic and morphometric data on Recent gars and my efforts in this regard would simply produce duplication. The purpose of measurements in this account is to present a small number of proportions of dorsal head length for Recent species to be compared with similar proportions obtained from fossils. Dried, articulated material was used exclusively with two exceptions—if the Recent species is not well known (*A. tristoechus*, *A. tropicus*), or if less than 8 articulated skulls were available. The measurements used in this study, their abbreviations, and their definitions are listed below. Measurements were taken to the nearest 0.1mm.

**DHL (Dorsal head length):** from the most anterior end of enameloid development of the premaxillary process to posterior junction of the parietals.

**MHL (Medial head length):** from the anterior tip of the rostrum to posterior junction of the operculum and suboperculum.

**SL (Snout length):** from the anterior tip of the rostrum to orbital edge of the anterior medial circumorbital.

**PS (Post snout length):** from orbital edge of the anterior medial circumorbital to posterior junction of the opercular and subopercular.

**MSW (Maximum snout width):** distance across the snout at junction of the posterior infraorbitals and the anterior lacrimals.

**LSW (Least snout width):** distance across the snout at junction of the anterior infraorbitals and the antorbitals.

**PL (Parietal length):** distance between anterior and posterior junctions of the parietals.

**FL (Frontal length):** distance between posterior and anterior junctions of the frontals.

**PmL (Length of premaxillary proc-**

ess): distance from posterior junction of the processes to anterior end of surface ornamentation.

LLJ (Length lower jaw): from symphysis to end of the angular.

OrW (Orbit width): distance between the orbits across top of the skull.

OrD (Orbit diameter): maximum distance across the orbit.

OpW (Opercular width): from posterior junction of the opercular and subopercular anterior to the end of surface ornamentation.

#### SYSTEMATIC METHODOLOGY

Gar relationships are evaluated using Hennig's (1966) method of phylogenetic analysis under the philosophy of deductive hypothesis testing advocated by Popper (1968a, 1968b). Popper's approach dictates adoption of an empirical methodology and the attitude on the part of the investigator that he attempt to falsify rather than confirm his hypotheses. Hypotheses which have not been refuted are said to be corroborated, and the degree of corroboration is directly related to the number and severity of valid tests applied to them. Where conflicting hypotheses compete because none is totally falsified by the evidence at hand, the hypothesis that has been rejected the least number of times is preferred (Wiley, 1975). Regardless of the number of times a hypothesis is corroborated, it is never considered confirmed. Rather, a hypothesis must always remain falsifiable and thus subject to refutation if it is to remain a part of science.

The phylogenetic methodology of Hennig (1966) has been extensively discussed by its proponents (Hennig, 1950, 1966, 1975; Brundin, 1966, 1968; Schlee, 1969, 1971; Nelson, 1969a, 1969b, 1970, 1971, 1972a, 1972b, 1973a, 1974; Crowson, 1970; Farris et al., 1970; Griffiths, 1972, 1973; Cracraft, 1974, 1975; Wiley, 1975) as well as its critics (Colless, 1967, 1969a, 1969b; Mayr, 1969, 1974; Darlington, 1970; Bock, 1973; Ashlock, 1971,

1973, 1974; Sneath and Sokal, 1973; Sokal, 1975; and others). I do not intend to discuss all the merits of the arguments presented by these authors. However, where criticisms of the phylogenetic method have proven valid, that part of the methodology has been de-emphasized or dropped; this does not invalidate the methodology (for example, the "deviation rule," Schlee, 1971; the "biographic" or "progression" rule, Croizat et al., 1974, and Nelson, 1974). Other objections have proved insubstantial or have been successfully answered by proponents of the methodology (for example, Mayr's 1974 objections are answered by Rosen, 1974b, and Hennig, 1975). There are two alternative methodologies. The evolutionary taxonomic method of Simpson (1961), Mayr (1969), and others is not used here because in the only instances in which it differs from Hennig's methods the evolutionary taxonomic methods result in untestable hypotheses (Wiley, 1975). The other possible alternate, numerical taxonomy (Sneath and Sokal, 1973), is not used here because it is concerned with phenetic, not phylogenetic, relationships.

Hennig's major phylogenetic principles may be summarized briefly. Species or groups of species are related by relative recency of common ancestry. Other criteria, such as overall resemblance or occupation of similar "adaptive zones," are rejected as grouping criteria. Taxa that share an immediate common ancestor are termed sister groups, and, since they originate from a splitting of the common ancestral species, they have the same time of origin. Only those features (characters) of taxa that indicate immediate common ancestry are used to elucidate relationships between sister groups. Characters purporting to demonstrate sister group relationships (i.e., immediate common ancestry) are termed apomorphic characters, and taxa sharing these characters are said to have synapomorphic characters in common. Characters indicating a phyloge-

netic relationship but not a sister group relationship are termed plesiomorphic characters. Characters that do not demonstrate common ancestry at any level are termed nonhomologous characters. Neither plesiomorphous nor nonhomologous characters are permitted in the analysis because they do not pertain to the problem at hand: the elucidation of immediate common ancestry between taxa. Taxa must be monophyletic in the strict sense, that is, descended from a single ancestral species and including all descendents of that species. Ancestors are not identified but remain hypothetical. Finally, classifications derived from phylogenetic hypotheses must reflect fully the relationships of the phylogenetic hypotheses. This principle dictates that sister groups have coordinate positions, and therefore coordinate ranks, in the classification, because they have the same time of origin.

I will consider three aspects of this methodology in depth. The relationship between a phylogenetic concept of homology and the terms apomorphic, plesiomorphous, and nonhomologous are discussed. The uses of characters for testing phylogenetic hypotheses under Popper's philosophy of deductive hypothesis testing are outlined. Finally, the integration of fossil and Recent taxa into a single analysis and classification is discussed.

*Homology.*—A concept of homology is basic to any methodology that makes comparisons between two or more organisms or taxa. In a general sense, characters that can be validly compared in studying relationships among organisms are considered homologues, whereas invalid comparisons involve nonhomologous characters. This is not to say that non-homologues cannot be validly compared in problems not concerned with relationships. For example, comparisons of bat and bird wings may be perfectly valid to an investigator interested in comparing two kinds of vertebrate flight dynamics.

The definition and use of the term homology depends largely on the aims and interests of the investigators employing the term. If one wishes to study only the phenetic relationships among taxa, then one will use a phenetic definition of homology (Sneath and Sokal, 1973). Those interested in phylogenetic relationships will adopt a phylogenetic definition (Simpson, 1961; Bock, 1969; Hennig, 1966). I have argued that a phylogenetic definition of homology is preferable to a phenetic definition because it leads to hypotheses of homology that contain all the potential falsifying observations of phenetic similarity and dissimilarity and all the potential falsifiers provided by rejection or corroboration of the phylogenetic hypotheses with which the homologies are associated (Wiley, 1975).

In this study, two or more characters are said to be homologous if they are transformation stages of the same original character present in the ancestor of the taxa displaying the character (Wiley, 1975, modified from Hennig, 1966). There are two logical derivations of this definition. First, characters that are derived in the immediate common ancestor of the taxa compared, and retained in these taxa, may be termed synapomorphic characters. Such characters are hypothesized as having originated in the immediate ancestral species as unique, or autapomorphic, characters. The presence of these characters in the descendent taxa is evidence of immediate common ancestry of the descendent taxa. Second, characters that are derived in an ancestor more genealogically distant than the immediate common ancestor, and retained in all subsequent common ancestors of the taxa in question, may be termed symplesiomorphic characters. Symplesiomorphies are not evidence of immediate common ancestry of the taxa considered because they are not unique to the immediate common ancestor of the taxa under consideration. Similar characters hypothesized not to be

present in the immediate common ancestor of the descendent taxa but present in two or more of the descendent taxa may be termed nonhomologous characters. Convergent and parallel characters are here considered nonhomologous.

Whether a particular homologous character is considered a plesiomorphy or an apomorphy depends on the level of universality of the phylogenetic hypotheses with which the character is associated as a subset. A phylogenetic hypothesis at the highest level of universality would incorporate all species of organisms known or recognized. All characters associated with this hypothesis as subsets would be synapomorphies, because all hypothetical immediate common ancestors would be present in the analysis. Thus, characters would be incorporated into the hypothesis at the point where they originated and all homologous characters would be synapomorphic. Plesiomorphies would not be proper subsets in such an hypothesis because all homologous characters would already be incorporated into the hypothesis where they exist as synapomorphies. Incorporation of a plesiomorphy would mean that a single homologous character had been used twice in the same analysis. But, no one has attempted to produce a hypothesis of the highest universality. Rather, subsets of this phylogeny are evaluated. For example, the lowest level of universality (if species are taken as the minimal taxonomic units) would be a phylogenetic hypothesis concerning the relationships of three species. Between the lowest and highest levels of universality are phylogenetic hypotheses of varying levels of universality. The level of universality a given hypothesis occupies depends on the number of taxa levels it incorporates; an hypothesis incorporating four species exists on a higher level of universality than one incorporating three species.

At any level of phylogenetic universality other than the highest both plesiomorphous and apomorphous characters

must be considered, because the investigator must sort out those characters in the organisms that demonstrate immediate common ancestry from those that do not. This may be framed as a question: which characters are uniquely derived in ancestors included in the hypothesis and which characters are uniquely derived in ancestors not included in the hypothesis, but retained by one or more ancestors included in the hypothesis? The synapomorphies of a phylogenetic hypothesis are the characters demonstrating immediate common ancestry at the level of universality considered. Sympleisomorphies differ in that they supposedly demonstrate immediate common ancestry at a level of universality higher than the hypothesis under consideration. Thus, sympleisomorphies are relevant to a larger phylogeny (as synapomorphies) containing the phylogeny under consideration as a proper subset. For example, the character "tetrapod limb present" belongs, as a synapomorphy, to the level of universality of the sarcopterygian amphibians and their sister group, the amniote sarcopterygians ("reptiles", etc.). This character would not provide a valid corroboration of the hypothesis that lizards were more closely related to rhynchocephalians than they were to snakes. This is because the character has already been used to test the proposition that the tetrapod sarcopterygians are all more closely related to each other than is any to the rhipidistian sarcopterygians. The use of this character to test the snake-lizard-rhynchocephalian hypothesis is an example of the use of a homology to test a phylogenetic proposition at the wrong level of universality. Homologies applied at the wrong level of universality provide invalid tests of phylogenetic hypotheses.

Autapomorphous characters properly belong only to species. (This statement is made under the assumption that species can be considered individuals as Ghiselin, 1974, has suggested. If however, species must be thought of as

groups of individuals then I think that autapomorphies would properly belong only to individual organisms and that the "autapomorphy" of a species is only the synapomorphy uniting its component individuals.) When the term is applied to a character of a higher taxon, it is only because that higher taxon is considered a single entity for the purpose of testing an hypothesis of relationship and is really being applied to the hypothetical ancestral species of the members of that taxon. When used in this way, it has some of the same properties as a plesiomorphy in that it cannot elucidate problems of immediate ancestry between the taxa considered, and it is an untestable homology (because the ancestor is not observed). Two further characteristics are apparent—its nature does not change as the level of universality is raised (like a synapomorphy), and its nature does change with a lowering of the level of universality (like a synapomorphy), but it does not immediately change to a symplesiomorphy, but to a synapomorphy. At a level at which it is synapomorphous, it is both testable as an homology and pertinent to elucidation of common ancestry.

When the term autapomorphy is applied at the species level, it is simply a unique character. There seems to be no phylogenetic argument that can be applied to test a unique character as derived other than by showing it to be a member of a synapomorphous pair. Thus, unique characters are accepted as apomorphous only by parsimony. Because parsimony does not constitute a test of a scientific hypothesis, I conclude that autapomorphies, like symplesiomorphies, are not testable propositions and cannot themselves be applied as tests of phylogenetic hypotheses.

Each hypothesis of synapomorphy is tested in a two-step process. First, it may be tested by its own set of potential falsifiers, without reference to the phylogenetic hypothesis with which it is associated as a proper subset. Most potential

falsifiers in this round of testing are similarities and differences, morphological or otherwise (Wiley, 1975). In the second stage of testing, the hypothesis of synapomorphy is associated with an hypothesis of phylogeny, and the phylogeny and synapomorphy are tested with other hypotheses of synapomorphy. If these other hypotheses of synapomorphy refute the phylogeny, they also refute the supposed synapomorphy unless one of two conditions is found: (1) the refuting "synapomorphy" is actually a symplesiomorphy, or (2) that the refuting "synapomorphy" is actually a non-homology. Neither of these types of characters represent valid tests (for reasons discussed above) and thus neither can refute the phylogenetic hypothesis (Wiley, 1975). If other hypotheses of synapomorphy are congruent with the phylogeny and its associated synapomorphy, then both hypotheses (phylogenetic and homologous) are said to be corroborated.

The refutation of a character as a synapomorphy and corroboration of that character as a symplesiomorphy can only be accomplished by raising the level of universality of the problem at hand either by finding the character in the sister group of the entire system tested, by finding the character so commonly outside the group that it is considered a symplesiomorphy, or by applying a developmental or ontogenetic rule of character transformation. Such a rule automatically raises the level of phylogenetic inquiry, for such rules are held only because they are common to large numbers of organisms outside the group of immediate interest.

*Testing phylogenetic hypotheses.*—All statements of phylogenetic relationships involve a minimum of three taxa at the lowest level at which they can be tested. Such hypotheses usually take the form that two taxa are said to share a common ancestor not shared by the third taxon. This relationship can be expressed by a phylogram. The distribu-

tion of characters among the three taxa provides deductive tests of the relationship. Without reference to Hennig's specific method but with reference to any test of relationship, we may say the only tests that can be considered valid attempts to refute a given three-taxon problem are those involving a single character present in two and only two of the three taxa. This is because only such a character is capable of refuting a given hypothesis of relationship. Characters shared by all three taxa or characters unique only to one are congruent with the four possible testable hypotheses for any three taxa. In a purely phenetic system, all shared characters, whether primitive or derived, have equal status in discussions about which branching diagram should be adopted as most parsimonious. Hennig's (1966) method differs fundamentally from a purely phenetic method in that all the shared characters are not used to refute a given relationship; only synapomorphous characters are used. Such testing can be accomplished only in an open system, that is, by considering taxa outside the three (or more) taxon system. Such considerations may be termed outgroup comparisons. The one condition placed on this procedure is that the three (or more) taxa must form a monophyletic group. The designation of outgroups for comparison permits an investigator to sort out which of the observed characters are unique to the three taxon system and which characters have a more general distribution. The outgroup comparison automatically raises the level of universality of the phylogenetic hypothesis to a new level. And, it allows the investigator to put his three-taxon problem in context with an hypothesis of a higher level of universality. The most parsimonious phenetic solution without reference to the outgroup may not necessarily be the most parsimonious phylogenetic solution within the context of the higher level phylogeny. So, to achieve overall parsimony, the phylogenetic in-

vestigator will have to reject certain characters as valid indicators of relationship (G. F. Engelmann, pers. comm.). And, it is the characters analyzed as symplesiomorphies or nonhomologies that can be objectively rejected as valid indicators of relationship within the three-taxon problem. This is because they are not pertinent to the elucidation of immediate common ancestry (as discussed above), and that acceptance of plesiomorphies as valid indicators within the context of the higher level phylogeny would lead to rejection of the three-taxon unit as a monophyletic group; this would violate the basic condition of the validity of the investigation itself. Synapomorphies, then, are the only valid tests of a phylogenetic hypothesis, and this testing is carried out as discussed above in the paragraph about testing synapomorphies. It should be pointed out here that a synapomorphy which is used to produce a phylogenetic hypothesis via "induction" does not test that phylogeny. Only after the phylogeny is proposed do synapomorphies provide deductive tests. Finally, when a situation exists where all hypotheses have been rejected, then that one which has been rejected the least number of times is preferred on the basis of parsimony.

*Integrating Fossil and Recent taxa.*—

Two problems are relevant here. First, can fossil and Recent taxa be integrated into the same analysis and classification? Second, should ancestor recognition be attempted if fossil and Recent taxa are integrated into the same analysis?

Patterson and Rosen (in press) have concluded that fossil and Recent taxa can be integrated into the same analysis and classification and that the objections of Hennig (1966) and Crowson (1970) can be overcome by considering fossil taxa as terminal branches. Further, they have outlined two conventions permitting a classification of both fossil and Recent taxa that exactly reflects the phylogenetic relationships of all taxa in the classification. These conventions are out-

lined in the classification of gars presented below. I conclude from their discussion that the integration of fossil and Recent taxa is possible with the phylogenetic methods of Hennig (1966).

Regarding recognition *vs.* non-recognition of ancestors, two questions are relevant. First, can ancestral taxa be supraspecific taxa or must they be species or populations? Second, can any particular hypothesis of ancestor-descendent relationship be tested in an objective manner?

The question of whether supraspecific ancestors can be recognized is closely tied to the definition of monophyly adopted. The concept of monophyly *sensu* Hennig (1966, or if one prefers, Hennig modified *sensu* Ashlock, 1973) leads to the logical corollary that supraspecific taxa cannot be considered ancestors because some of the members of the "ancestral" taxon would actually be more closely related to taxa outside the group than to taxa inside the group. On this basis I would agree with Patterson and Rosen (in press) that ancestral units, if recognized, must be species or populations and not supraspecific groups. One might argue, however, that Hennig's definition of monophyly is not preferred.

Hennig's concept of monophyly has at least three points which, in my opinion, make it superior to concepts of monophyly outlined by Simpson (1961), Ashlock (1971), and Mayr (1974). The first point concerns the evolutionary process. What little we know of evolutionary process indicates that populations are the highest level taxa that evolve and species are the highest level taxa that can be considered populations. Since higher taxa do not evolve, they cannot be considered ancestral units. The reality of higher taxa is based solely upon whether they are accurate reflections of past speciation events and thus higher taxa are historical constructs and have no reality as active units of evolution. The second point concerns the concept of group

membership. Hennig's (1966) definition of monophyly dictates that all the descendants of an ancestor be placed in the same group as the ancestor. This conforms to basic set theory and is methodologically precise. The removal of a species or group of species from a taxon that includes its ancestor and sister group and then calling the original group monophyletic and ancestral to the species or group of species is untenable because, firstly, it breaks up a logical set of two logical subsets into one logical set (the species or group of species, the "s" group of Ball, 1975:413) and one illogical set (the "ancestral" taxon, whose general components can no longer be defined, the "s-bar" group of Ball, 1975:413), and, secondly, it makes the term monophyly an open term, that is, any taxon could be termed monophyletic (Hennig, 1966). Thirdly, Rosen (1975) has pointed out that use of non-monophyletic groups *sensu* Hennig (1966) in biogeographic analysis leads to apparently incomplete distribution patterns because some species, or groups of species, are not classified with their nearest relatives. This leads to an underestimation of the ancestral range of the hypothetical common ancestor of the non-monophyletic group. Thus, adoption of an evolutionary taxonomic definition, such as that of Simpson (1961), obfuscates biogeographic analysis.

Two of Hennig's original premises are that ancestors (=ancestral species) remain hypothetical and that the search for ancestors is futile. Hennig specifically rejected the idea that ancestor-descendent relationships between two or more species could be scientifically demonstrated in either the phyletic sense (A gives rise to B through time without a geographic isolation event) or the cladistic sense (A gives rise to B and C by splitting). Nelson (1970a, 1973a) and Cracraft (1974) state that ancestors are empirically unknowable.

Whether this position or Bock's (1973) assertion to the contrary is correct

will not be taken up here for three reasons: (1) my thinking on these questions has been influenced by my colleague George Engelmann and thus is better left for a future joint paper; (2) those species of gars diagnosed without autapomorphies and thus which might in some circumstances be considered possible ancestors are so fragmentary that hypotheses of ancestry can be put aside for lack of information; (3) all other fossil gars studied are derived, and questions of specific ancestors never came up in the analysis. I will state, as an unsupported conjecture, that hypotheses of ancestry relating to this study of gars are trivial hypotheses and were not pursued.

#### BIOGEOGRAPHIC METHOD

The panbiogeographic or "vicariance" method is used to describe certain distributional patterns among gars. This methodology has been extensively discussed by its originator, Croizat (1958, 1962), and summarized by Croizat, Nelson, and Rosen (1974) and Rosen (1974a).

The vicariance method attempts to find general patterns of distribution to provide a general solution to explain the individual species pattern in the most economical manner. This is accomplished by track analysis. A track is a line around the range of a species or enclosing the various ranges of the taxa of a monophyletic group. When more than one species is enclosed within the track, then the track is an estimate of the range of the ancestor of the monophyletic group. Tracks enclosing non-monophyletic groups, such as paraphyletic groups, are not as informative as those enclosing monophyletic groups because they enclose only part of a monophyletic group and therefore underestimate the range of the common ancestor of the taxa included within the track.

Analysis begins by plotting as many as possible of the tracks observed and looking for general distributional patterns, that is, those comprising more

than a single track. Such general distributional patterns are termed generalized tracks. The more individual tracks making up the generalized track, the more corroborated the generalized track. Additionally, generalized tracks made up of a number of distantly related taxa are more highly corroborated than generalized tracks with the same number of individual tracks made up of closely related taxa. The generalized track estimates an ancestral biota in the same way an individual track estimates the ancestral range of the ancestral species of the monophyletic group.

The presence of a generalized track rejects the hypothesis that the individual tracks comprising it could have originated by the independent chance dispersal of, or migration of, each individual species comprising the track. This is because it is assumed that the chances of a general distributional pattern emerging from the independent dispersal of many component species which have different biological needs and dispersal capabilities is nil. Instead, a generalized track calls for explanation on a general level. That is, it calls for an explanation that involves the biota as a whole to produce the observed pattern, rather than separate explanations involving each member of the biota individually.

The vicariance method recognizes the reality of dispersal. Dispersal is identified in one of four ways: (1) by the overlap of generalized tracks, (2) by the observation that a species or group of species does not conform to any generalized track, (3) by direct observation of dispersal or migration and subsequent settlement, and (4) by sympatry between sister groups. All of these methods of identifying dispersal except (3) are founded on the assumption that the process of speciation is usually allopatric.

#### THE RELATIONSHIP OF GARS TO OTHER ACTINOPTERYGIANS

Gars traditionally have been considered primitive actinopterygian fishes, but

their exact sister group relationships have been subject to dispute. Müller (1844) included the gars and *Amia* with the polypterids in his order Holostei. Huxley (1861) removed the polypterids from the Holostei and placed them in the Crossopterygii. This alignment of *Amia* and gars was accepted by most workers of the nineteenth century and has most recently been advocated by Nelson (1969a) and Jessen (1972, 1973). Others have argued that *Amia* is more closely related to teleosts than to gars and that Holostei is a grade or paraphyletic group (Westoll, 1944; Gardiner, 1960, 1963, 1967; Jollie, 1962; Patterson, 1973). When fossil fishes are considered, gars have been considered by most workers as being most closely related to semionotiforms (Goodrich, 1909, 1930; Rayner, 1941, 1948; Gardiner, 1960, 1963, 1967; Romer, 1966) or aspidorhynchids (Reis, 1887; Goodrich, 1904). These conclusions were challenged by Patterson (1973) who argued that semionotiforms are more closely related to halecomorphs (*Amia*) and teleosts than to gars, and that aspidorhynchids are teleosts.

In assessing the relationships of gars to other actinopterygians, I attempted to establish which of the characteristics of gars are autapomorphic, which are synapomorphic with one or more non-gar actinopterygian groups, and which are symplesiomorphic or nonhomologous and thus of no value in assessing phylogenetic affinities. Three major anatomical areas are covered: the skull, the visceral arches, and the post-cranial skeleton.

Four major hypotheses of gar relationships are tested:

- (1) Gars and *Amia* are sister groups and are more closely related to teleosts than are chondrosteans (Nelson, 1969a; Fig. 1a).
- (2) Gars and *Amia* are sister groups and chondrosteans are the sister group of teleosts (Jessen, 1972; Fig. 1b).

- (3) *Amia* is the sister group of teleosts and gars are more closely related to this group (halecostomes) than are chondrosteans (Patterson, 1973; Fig. 1c).
- (4) Semionotids are the sister group of gars and this group the sister group of amiids and teleosts (Westoll, 1944 and others cited above; Fig. 1d).

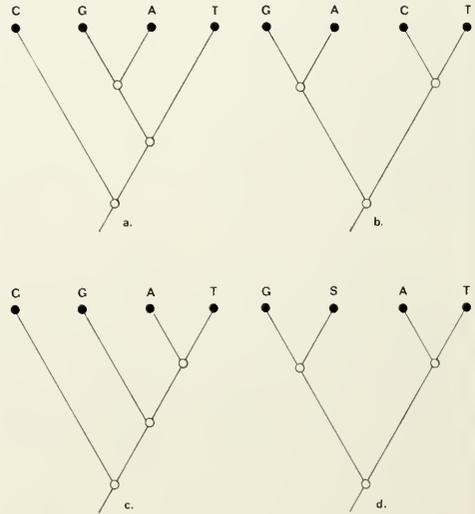


FIG. 1.—Four hypotheses of the relationships between chondrosteans (C), gars (G), amiids (A), teleosts (T), and semionotids (S). a. after Nelson (1969a); b. after Jessen (1972); c. after Patterson (1973); d. after Rayner (1948).

### THE SKULL

The pattern of dermal and endochondral ossifications is basically similar in gars, other neopterygians, and in many chondrosteans, making hypotheses of homology possible (Patterson, 1973:239). The pattern of dermal ossification of gars is illustrated in Fig. 2.

The ethmoid region of gars differs from those of other actinopterygians in being elongated to produce the characteristic lepisosteid snout. There are no ethmoid ossifications. Patterson (1975: 499) reviewed the occurrence of ethmoid ossifications in various actinopterygian groups and concluded that ethmoid ossifications are primitive for osteichthyans.

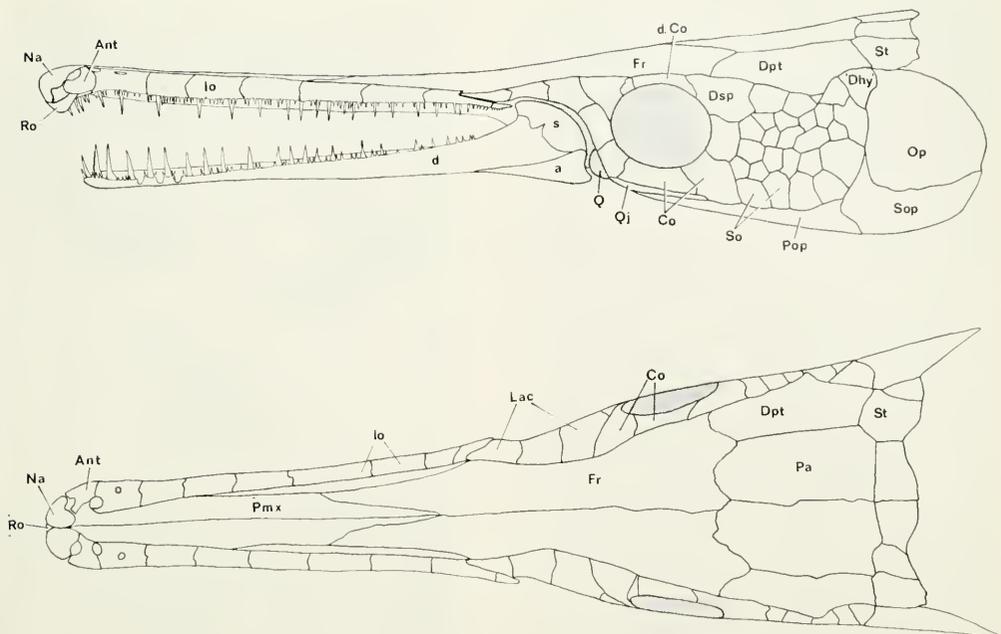


FIG. 2.—Lateral (upper) and dorsal (lower) views of the skull of *Lepisosteus oculatus* (LACM 33916-3). a, angular; Ant, antorbital; Co, circumorbital; d, dentary; d Co, dorsal circumorbital; 'Dhy', "dermohyal"; Dpt, dermo-phenotic; Fr, frontal; Io, infraorbital; Lac, lacrimal; Na, nasal; Op, opercular; Pop, preopercular; Q, quadrate; Qj, quadratojugal; Ro, rostral; s, surangular; So, suborbital; Sop, subopercular; St, supratemporal.

Lateral ethmoids are found in teleosts, *Amia*, large *Acipenser*, *Polypterus*, and *Latimeria* (Patterson, 1975). They are also found in palaeoniscids (*Bergeria*, Nielsen, 1949; *Perleidus*, Patterson, 1975), fossil halecomorphs (*Caturus*, Rayner, 1948; *Sinamia*, Stensiö, 1935), "holosteans" (*Macrepistius*, Schaeffer, 1971; *Lepidotes*, Patterson, 1975). Fully ossified forms, such as some paleoniscids, all parasemionotids, and the semionotiforms *Heterolepidotes* and *Dapedium*, probably had internal ossified ethmoids during development (Patterson, 1975:499). I conclude that the elongation of the ethmoid cartilage and the lack of ossifications in this cartilage are synapomorphic characters shared by gars.

Gars and palaeoniscids lack an endoskeletal rostrum of the type seen in Recent chondrosteans, saurichthyids, amiids, and teleosts. Independent ossi-

fications of this cartilage are known only in *Amia*, pachycormids, and Recent teleosts, but could have been present during the ontogeny of solidly ossified forms such as saurichthyids, pholidophorids, *Dapedium*, and *Heterolepidotes* (Patterson, 1975:502). Patterson (1975) concluded that (1) an endoskeletal rostrum with a well defined nasal septum and laterally or dorsally oriented nasal pits was independently derived in several lineages and that lack of this cartilage is plesiomorphic for actinopterygians, and (2) an endochondral rostral bone in front of the lateral ethmoids is synapomorphic for halecostomes (the pre-ethmoids of *Amia* and *Pachycormus*, the supra-ethmoids and ventral ethmoids of teleosts).

The dermal components of the lepisosteid snout consist of a medial rostral, paired nasals and antorbitals, underlain by the premaxilla and paired vomers.

The number and position of dermal snout elements have been discussed by many authors. Gardiner (1963) concluded that the primitive pattern of ossification consisted of a postrostral separating the nasals and a pair of compound rostro-premaxillo-antorbitals. Schaeffer (1973) suggested that there was a medial rostral as well as postrostral. Wenz (1968) concluded that evidence did not permit a primitive *bauplan* for the actinopterygian snout to be established, and Patterson (1975) apparently agreed. Although the snout ossifications of chondrosteans are variable, the pattern within the Neopterygii is more stable and permits unambiguous comparisons. Gars are similar to other neopterygians in having a medial dermal rostral which carries the ethmoid commissure of the infraorbital canals, paired nasals which contact each other and carry the supraorbital canals, and separated antorbitals which carry the infraorbital canals. These are underlain by paired premaxillaries and vomers. The rest of the snout is overlain by the ascending processes of the premaxillaries and the frontals. Both pairs of bones carry the supraorbital sensory canal. The snout is bordered by a series of toothed infraorbitals that carry the infraorbital sensory canal.

Gars differ from other actinopterygians in having two commissures between the supraorbital and infraorbital sensory canals (Fig. 3a). The first is produced by a backward bending of the supraorbital canal on the nasal. This commissure joins the two sensory canals between the nares and traverses the nasals and antorbitals. The second commissure is a branch of the infraorbital canal that runs from the antorbital to the premaxillary arm posterior to the nares (Jollie, 1969). Jollie (1969) stated that this condition is unique among actinopterygians and has suggested that the internarial commissure is homologous with that in *Polypterus* and *Acipenser* but not homologous with the internarial commissure in *Amia* (which

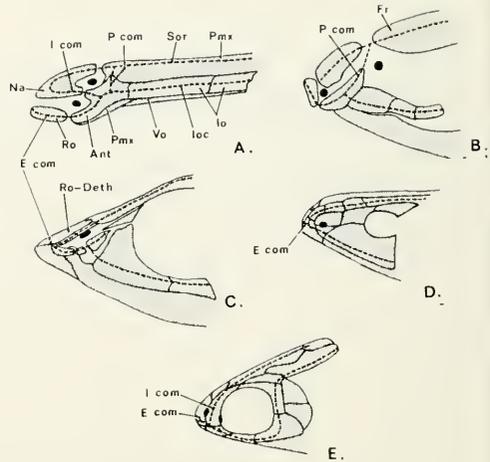


FIG. 3.—Lateral view of the snout of five osteichthyan fishes. A. *Lepisosteus* after Jollie, 1969; B. *Amia* after Jollie, 1969; C. *Elops* after Forey, 1972; D. *Eusthenopteron* after Stensiö, 1947; E. *Pteronisculus* after Stensiö, 1947. Ant, antorbital; E. com, ethmoid commissure; Fr, frontal; I. com, internarial commissure; Io, infraorbital; Ioc, infraorbital canal; Na, nasal; P. com, postnasal commissure; Pmx, premaxilla; Ro, rostral; Ro-Deth, rostro-dermethmoid; Sor, supraorbital sensory canal; Vo, vomer.

runs between the nares but does not involve the nasal and develops late in ontogeny, Fig. 3b). The teleostean snout has a single commissure, which is a branch of the infraorbital canal traversing the antorbital (as in *Amia*) and either connects with the supraorbital canal posterior to the nares (osteoglossids, Nelson, pers. comm.) or ends before meeting the supraorbital canal (*Elops*, Nelson, 1969c; Fig. 3c).

These differences are best assessed by surveying patterns of sensory canals and commissures among other gnathostomes. In the snout of sharks, the primitive pattern may be that of *Chlamydoselachus*, in which the infraorbital and supraorbital canals meet behind the nares (Jollie, 1969). In acanthodians the supraorbital canal is joined to the infraorbital canal anterior to the orbit, but the relationship of the commissure to the nares is apparently unknown (see Watton, 1937). Among sarcopterygians there

are several snout patterns. The dipnoans *Protopterus* (Panchen, 1967) and *Neoceratodus* (Stensiö, 1947) have no commissures between the supraorbital and infraorbital canals but each is connected via a commissure to its counterpart across the snout. In rhipidistians (Fig. 3d) there is a single commissure between the supraorbital and infraorbital canals in front of the snout, and the infraorbital canals are connected to each other across the snout (*Holoptychius*, Jarvik, 1947; *Eusthenopteron*, Jarvik, 1944; see Stensiö, 1947, for summary but note that figure 29b, p. 106 is probably incorrect). In *Latimeria chalumnae* there are commissures between the supraorbital and infraorbital canals both anterior to the nares and between the nares (Millot and Anthony, 1958; Jollie, 1969). In at least one fossil coelacanth (*Nesides schmidti*) there is no indication of an internarial commissure. I note that *Polypterus* displays the sarcopterygian pattern (see Jollie, 1969, and Stensiö, 1947, for illustrations).

Within the Actinopterygii the primitive condition (Fig. 3c) seems to be that in which the infraorbital and supraorbital canals are connected by an internarial commissure and the infraorbital canals on each side of the head are connected via the rostral commissure (Gardiner, 1963; Jollie, 1969). This condition is found in *Pteronisculus* (Nielsen, 1942), *Bergeria* and *Australosomus* (Nielsen, 1949), *Moythomasia* (Jessen, 1968), *Ategotrachelus*, *Kentuckia* and others, but not in *Canobius* and *Babastrania* (Gardiner, 1963). This snout sensory canal pattern is probably apomorphic for the Actinopterygii and thus plesiomorphic within the group. What the plesiomorphic pattern is for teleostomes in general is not clear. The pattern seen in the coelacanth *Latimeria* incorporates both the rhipidistian and actinopterygian patterns. Dipnoans have a different, and presumably apomorphic, pattern. But whatever the basic teleostome pattern may be, it is logical

to assume that the internarial commissure between the supraorbital and infraorbital canals seen in gars is homologous with the same commissure seen in most chondrosteans. And, the presence of a postnarial commissure between these sensory canals is hypothesized to be apomorphic for taxa within the Actinopterygii. Two questions remain: (1) is the internarial commissure of *Amia* homologous to the internarial commissure of gars and chondrosteans?; and (2) what are the homologies of the postnarial commissures of gars and teleosts? Jollie (1969) stated that the internarial commissure of *Amia calva* is not fully developed until relatively late in development (200 mm). Allis (1889) figured the early development of the commissure. In 10 mm specimens of *Amia calva* the commissure has the same orientation as adult *Elops*, that is, the branch of the infraorbital canal is directed upward and is behind the nares. It then contacts the edge of the posterior nares (11.5 mm), and, as the posterior nares move farther back during development, the infraorbital branch comes to lay between the nares. These ontogenetic changes corroborate a hypothesis that the internarial commissure of gars and *Amia* are non-homologous. Further, it corroborates a hypothesis of synapomorphy between the internarial commissure of *Amia* and the postnarial commissure of teleosts and gars. Thus it would seem that a postnarial commissure or an infraorbital branch on the antorbital is apomorphic for neopterygians. Gars are unique in having both the plesiomorphic and apomorphic commissures. *Amia* and teleosts lack the internarial commissure of gars and chondrosteans, an apomorphic condition. Further, *Amia calva* is autapomorphic in having the postnarial commissure between the nares.

The premaxilla of gars includes a toothed anterior part, the premaxilla proper, and the premaxillary or nasal process (pmx, Fig. 2, and Patterson, 1973) which makes up as much as 50% of the

length of the snout and carries the supra-orbital canal. Hammarberg (1937) contended that the supraorbital canal was found on the nasal process because two nasal ossification centers and their associated sensory placodes were incorporated into the nasal process. Thus, he concluded that the premaxilla is a compound bone composed of one anasmatic bone and parts of one sensory canal bone. He termed this bone the premaxillo-nasals (other names applied to the premaxilla of gars include the ethmonasals, Allis, 1905, and the naso-premaxillaries, Mayhew, 1924). Aumonier (1941) studied the premaxillary process and concluded that no nasal ossification centers were involved and that the association of the premaxillary process with the supraorbital canal was produced by simple posterior growth of the premaxillary arm. Further, he could find no evidence that the premaxilla arose from two ossification centers.

Patterson (1973) compared the premaxillary process of gars with that of *Amia* and he pointed out three basic similarities between the two: (1) both line the nasal pits, (2) both suture with the frontal, and (3) both are perforated by the olfactory nerve. He surveyed the distribution of nasal processes and found them in parasemionotids, semionotids, caturids, and amiids. The olfactory nerve perforated the nasal process in *Semionotus*, *Lepidotes*, and *Eurycarmus* (loc. cit.: 510). Patterson also found that the lateral dermethmoids of philodophorids occupy the same topographic position as the nasal processes of amiids and the fossils named above, and that these lateral dermethmoids differ from the nasal process and are primitively toothed. Patterson (1975) concluded that the premaxillary processes of all neopterygians are basically homologous and that premaxillary processes arose by backgrowth of the small process such as that seen in parasemionotids.

There are, however, differences between the premaxillary processes of gars

and *Amia*. Pehrson (1940) studied the ontogeny of the premaxilla of *Amia* and concluded that it was a compound bone composed of two ossification centers, the premaxilla proper and a posterior ossification center, the rhinal bone of Bjerring (1972). In contrast, the gar premaxilla has either a single ossification center (Aumonier, 1941:20), or is derived from an anasmatic bone and parts of a sensory bone (Hammarburg, 1937). Apparently, the developmental sequences of the premaxillae of *Amia* and gars differ. In addition, the premaxillary process of gars makes up a significant portion of the dorsal surface of the snout, whereas that of *Amia* and the semionotids I have examined lies beneath the nasals. Finally, parasemionotids, the presumed sister group of amiids, lack a well developed premaxillary process, and, unless parasemionotids are apomorphic in lacking a well developed process, we must assume that the common ancestor of all halecomorphs also lacked a well developed premaxillary process. Regardless of the significance placed on the topographic dissimilarity or developmental dissimilarity, the phylogenetic argument seems to refute the conjecture that the premaxillary process of gars and *Amia* is homologous. Whether the premaxilla of *Amia* is homologous to that of teleosts (Patterson, 1973) is also open to question, but I have no additional observations to add to those of Patterson (1973, 1975).

The vomers of gars are paired. This is apparently the plesiomorphous condition and is found in a variety of other actinopterygians (see Patterson, 1973). *Lepidotes*, some other semionotids, halecomorphs, and teleosts have a single vomer (Rayner, 1948), a character that refutes the ancestor-descendent or sister group relationship proposed by Rayner (1948) for gars and *Lepidotes* (Patterson, 1973). The vomers overlie the parasphenoid and the ectopterygoids. These bones will be discussed under the palatal section below.

The remainder of the dorsal snout is made up of the anterior half of the frontals bordered by a series of 5 to 10 toothed infraorbital bones and the atrophied maxilla. Both the long series of toothed infraorbitals and the atrophied maxilla are unique for gars and are considered synapomorphic for the group. In early growth stages the maxilla is much larger and occupies the correct topographic position of the normal actinopterygian maxilla. It begins to atrophy relative to other bones when the young reach about 26 mm total length (Hammarburg, 1937; Aumonier, 1941). *Lepidotes* has a small series of infraorbitals running onto the snout (Westoll, 1937), but these are neither toothed, nor as numerous as those of gars, nor do they border the snout margin. I conclude that a hypothesis of synapomorphy between the infraorbitals of gars and *Lepidotes* is a weak hypothesis and that the presence of non-toothed infraorbitals in *Lepidotes* is a plesiomorphous condition.

The dermal bones posterior to the snout of gars are the usual frontals, parietals, dermopterotics, supratemporals, and post-temporals dorsally, and the lacrimals, circumorbitals, suborbitals, and the opercular series laterally (see Fig. 2).

Gars differ from other actinopterygians in the relationships of the dermopterotic and dermosphenotic to their endochondral counterparts, the sphenotic and pterotic. Gars have a dermopterotic-sphenotic articulation with the distal end of the sphenotic frequently being seen externally under the lateral wing of the dermopterotic. If Patterson's (1975) hypothesis that the pterotic is present in gars and missing in amiids is correct (see discussion of neurocranium below), then gars have both the sphenotic and pterotic articulating with the dermopterotic and they have a dermosphenotic without an endochondral articulation. Amiids and teleosts differ in having an epioccipital-dermopterotic articulation and the usual sphenotic-dermosphenotic articulation primitive for actinopterygians.

And, amiids are unique in having lost the pterotic and thus in lacking a pterotic-dermopterotic articulation.

Behind the parietals and dermopterotics of actinopterygians is a supratemporal series that carries the extrascapular or supratemporal commissure between the supraorbital canals. Gars have two to six supratemporals on each side of the midline (Fig. 4b) whereas amiids and most teleosts have a single supratemporal on each side of the midline (Fig. 4c, d) (or, in some teleosts, a complete loss of the supratemporals). Palaeoniscoids such as *Moythomasia* (Jessen, 1968) and *Pteronisculus* (Fig. 4a, from Nielsen, 1942), branchopterygians (*Polypterus*, Daget, 1950), and a variety of sarcopterygians have two or more supratemporals on each side of the midline (Fig. 4a). I hypothesize that this condition is plesiomorphous. Within the Neopterygii, semionotiforms have two per side. A single supratemporal per side is found in the fossil halecomorphs (as figured from various sources by Lehman, 1966) *Parasimionotus* (Fig. 118), *Promecosomia* (Fig. 122), *Eoeugnathus* (Fig. 126), *Heterolepidotes* (Fig. 129), *Furo* (Fig. 128), *Caturus* (Fig. 133), *Oneoscopus* (Fig. 135), *Urocles* (Fig. 136), *Microsemius* (Fig. 143), *Ophiopsis* (Fig. 141). A single supratemporal per side is also found in *Pachycormus* (Lehman, 1966, Fig. 147); and in the philodophorids and leptolepids (but not in *Sinamia*, Lehman, 1966, Fig. 138). I hypothesize that a single supratemporal on each side of the midline is a synapomorphy uniting halecomorphs and teleosts.

Gars have a complete circumorbital ring ending anteriorly in three lacrimals, a condition regarded by Gosline (1965) as primitive (Fig. 2). Patterson (1973) found this conclusion premature. Some palaeoniscoids do not have a complete circumorbital ring. Rather, the nasals form the anterior borders of the orbits (*Pteronisculus*, *Boreosomus*, *Canobius*, and platysomids, Stensiö, 1947; *Poly-*

pterus, Jarvik, 1947). Others have a complete circumorbital series (*Cheirolepis*, Watson, 1925; *Discellopyge*, Brough, 1931). The most ancient semionotiform, *Acentrophorus*, has a complete circumorbital ring (Gill, 1923), as do other semionotiforms such as *Lepidotes* (Westoll, 1937), *Semionotus* (Lehman, 1966), *Dapedium* (Wenz, 1968). Thus, it appears that a complete circumorbital ring is primitive within the Neopterygii, regardless of its condition within Actinopterygii. I conclude that the secondary loss of some components of the circumorbital series is a synapomorphy uniting halecostomes.

The dermosphenotic carries the junction of the otic and postorbital portions of the infraorbital canal. In some gars the dermosphenotic is incorporated into the circumorbital ring, a plesiomorphous character shared with some palaeoniscoids, *Amia*, and teleosts.

The relationships of the supraorbital and infraorbital canals relative to the dermal roofing bones are variable within the Actinopterygii. In palaeoniscids there is, primitively, no commissure between the two canals (Fig. 4a). This condition is also seen in young *Amia calva* (Allis, 1889) and adult *Pholidophorus macrocephalus* (Patterson, 1975). In gars there is a commissure between the otic branch of the infraorbital canal and the supraorbital canal on the dermosphenotic (Fig. 4b). In *Amia* the commissure is further forward and involves the frontals (Fig. 4c). Teleosts primitively lack a commissure (pholidophorids, leptolepids, *Elops*, Fig. 4d), but more derived groups have a commissure (Gosline, 1965). The condition in gars (and perhaps *Amia* and some Recent teleosts) is apparently derived, and such commissures apparently have been derived independently in several lineages.

Gars have a mosaic of suborbitals between the circumorbitals and the opercular series (SO, Fig. 2). The presence of suborbitals is considered plesiomorphous by Schaeffer (1973) and Patterson

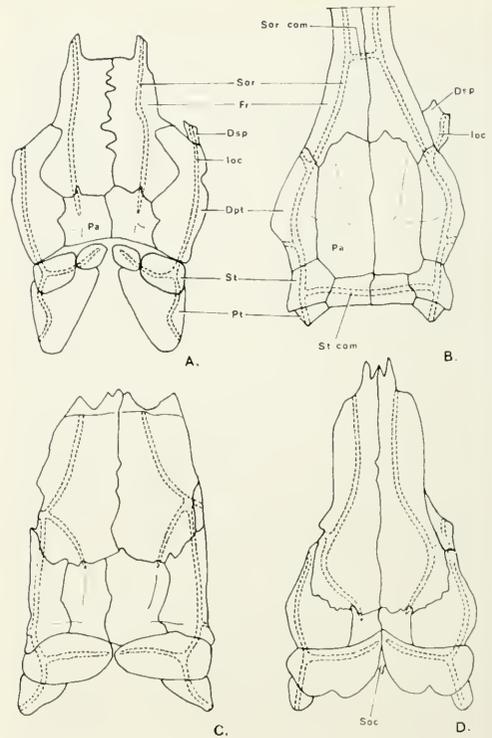


FIG. 4.—Dorsal view of the posterior skull roof of four actinopterygians. A, *Pteronisculus*, after Nielsen, 1942; B, *Lepisosteus*, after Patterson, 1973; C, *Amia* after Patterson, 1973; D, *Elops*, after Forey, 1972. Dpt, dermosphenotic; Dsp, dermosphenotic; Fr, frontal; Ioc, infraorbital canal; Pt, post-temporal; Soc, supraoccipital; Sor, supraorbital sensory canal; Sor com, supraorbital commissure; St, supratemporal; St com, supratemporal commissure.

(1973). They are found in a large number of palaeoniscids and fossil halecostomes (see Patterson, 1973, for discussion) but are missing in *Amia calva* and recent teleosts. Patterson (1973:245) interpreted this absence of suborbitals as evidence for relationship because, although some primitive teleosts (i.e. pholidophorids) have a few suborbitals, the parallelism is an "almost unique condition." I cannot accept this conclusion. A character that can demonstrate relationships is one found in the common ancestor of the taxa related. But most evidence leads to the conclusion that the common ancestor of amiids and teleosts had suborbitals and that primitive tele-

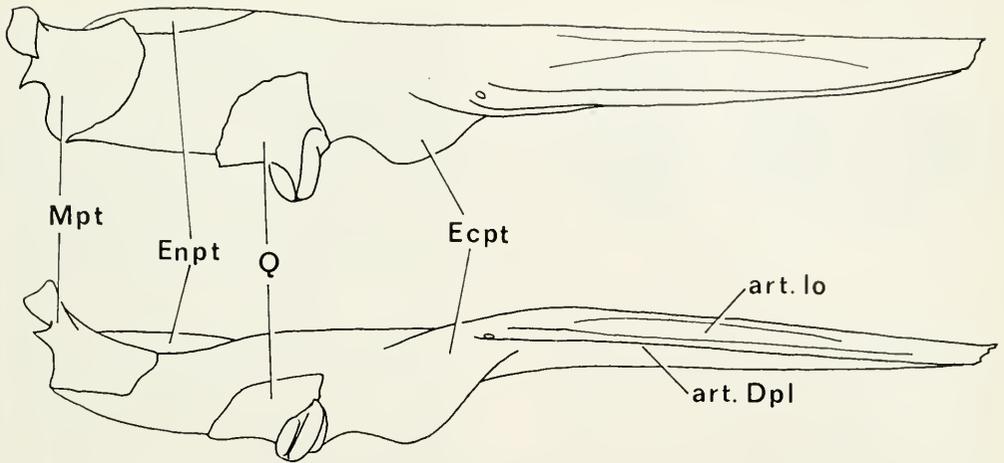


FIG. 5.—Pterygoid bones of *Atractosteus tristoechus* (USNM 111309). Upper, dorsal view; Lower, lateral view. Dermopalatine omitted. art. Dpl, articular surface of dermopalatine; art. lo, articular surface of infraorbitals; Ecpt, ectopterygoid; Enpt, endopterygoid; Mpt, metapterygoid; Q, quadrate.

osts (pholidophorids and leptolepids) retained this character. The absence of suborbitals is a parallelism and not a synapomorphous condition in spite of the uniqueness of the parallelism. Thus, it cannot be used to indicate a sister group relationship between *Amia* and teleosts.

Incorporated in the suborbital mosaic of gars is a bone identified by Jollie (1962) as the dermohyal (Dhy, Fig. 2). Patterson (1973:245) concluded that the evidence for identification of this bone is weak, and that, while it may be the dermohyal, it could be the homologue of the suprapreoperculum. I agree with Patterson and have been unable to determine if the bone is a dermohyal. The question has some phylogenetic significance, for if it is the dermohyal, then amiids and teleosts would share the synapomorphy of loss of the bone. If it is not the dermohyal, then gars share the loss with other neopterygians, making the character a synapomorphy of neopterygians.

The opercular series of gars includes the opercular, subopercular, and preopercular (Fig. 2). Gars lack an interopercular, as do palaeoniscids. Haleco-

morphs, semionotiforms, and teleosts have an interopercular, a synapomorphous condition relating them and excluding gars. Conjectures concerning the secondary loss of the interopercular of gars (Rayner, 1948) depend on the assumption that gars are the direct descendants of semionotiforms (McAllister, 1968). This assumption is rejected on the basis of other evidence (Patterson, 1973).

The palate of gars consists of elongate ectopterygoids overlain by toothed dermopterygoids (dermopalatines), endopterygoids, and metapterygoids (Fig. 5). Gars lack an autopalatine, an endochondral bone found in *Amia*, teleosts (Patterson, 1975), "Gogo palaeoniscoids" (Gardiner, 1973), *Pteronisculus* (Nielson, 1942), semionotids (Gardiner, 1960; Wenz, 1968), and acanthodians (Miles, 1973). Gars differ from other actinopterygians in that the metapterygoid is connected to the hyomandibular and preopercular only by cartilage and connective tissue.

The suspensorium of gars is unique in several respects (Fig. 6). The quadrate is supported entirely by the ectopterygoid medially and the quadratojugal posteriorly. The quadrate is situated in

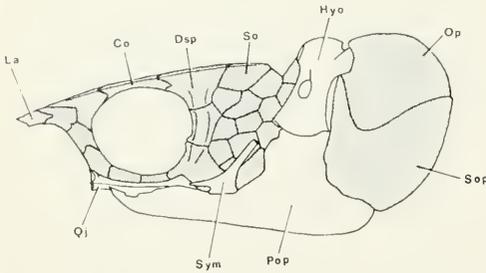


FIG. 6.—Medial view of the post-orbital region of *Atractosteus tropicus* (AMNH 27939). Suspensorial ossifications unstippled, other bones stippled. Co, circumorbital; Dsp, dermosphenotic; Hyo, hyomandibular; La, lacrimal; Op, opercular; Pop, preopercular; Qj, quadratojugal; So, suborbitals; Sop, subopercular; Sym, symplectic.

front of the orbit rather than behind. The symplectic is not in close association with the quadrate but is found far posteriorly on the preopercular.

Patterson (1973) reviewed the suspensorium of neopterygians and concluded that (1) the placement of the quadrate in front of the orbit is an autapomorphy of gars, (2) the loss of the quadratojugal and the double articulation of the lower jaw via both the symplectic and the quadrate was an apomorphy of amiids (including *Caturus* and *Furo*), and (3) the fusion of the quadrate and the quadratojugal is an apomorphy of teleosts. The separate quadratojugal of gars is a primitive character shared with *Lepidotes* (figured by Patterson, 1973). In many specimens of gars the quadratojugal makes up an external component of the skull and with the ectopterygoid provides the only ossified support of the quadrate. The symplectic of gars is "L" shaped and articulates only with the quadratojugal and the preopercular. The shape and topographic position of the symplectic of gars is unique among actinopterygians.

In regard to the teleostean condition of the quadrate and quadratojugal, Allis (1909) and Holmgren and Stensiö (1936), with Patterson (1973), identify the splint-like process of the teleost

quadrate as the quadratojugal. Fred Cochocki and I observed this process in the leptocephalus larva of *Elops saurus* (UMMZ 165213, 25 mm) before it fused to the quadrate. The splint-like bone was not associated with any cartilage and occupied the exact topographic position of the quadratojugal of *L. osseus* of the same length. In later stages of *Elops saurus* the process fuses with the quadrate. These observations corroborate the hypotheses of Patterson and other workers. The quadrate of teleosts, then, is a compound bone composed of one endochondral (quadrate) and one dermal (quadratojugal) element.

The hyomandibular of gars articulates with the auditory capsule of the neurocranium above the foramen for the lateral head vein and the ramus hyomandibularis VII. Like other actinopterygians there is an articulation with the opercular, and the hyomandibular fits into a groove of the dermopterotic. The position of the hyomandibular in relation to the lateral head vein and ramus hyomandibularis VII of actinopterygians agrees with that of *Polypterus* (Goodrich, 1930), acanthodians (Miles, 1968), and Paleozoic sharks (Schaeffer, 1967b). In dipnoans and Recent sharks the hyomandibular articulates below the foramen of the lateral head vein and ramus hyomandibularis VII, and this lower articulation was considered by Goodrich (1930) to be the plesiomorphous gnathostome condition. Schaeffer (1967b) and Gardiner (1973) disagreed, and stated that the plesiomorphous condition is a high articulation. If this is true, then the condition in Recent sharks may be a synapomorphy for that group.

The ramus hyomandibularis VII of actinopterygians passes medially to the hyomandibular and either penetrates the bone (palaeoniscids, neopterygians) or continues to pass laterally (*Acipenser*). In either case it does not branch into the mandibular and hyoid branches until it has either passed or penetrated the hyomandibular. In dipnoans (insofar as a

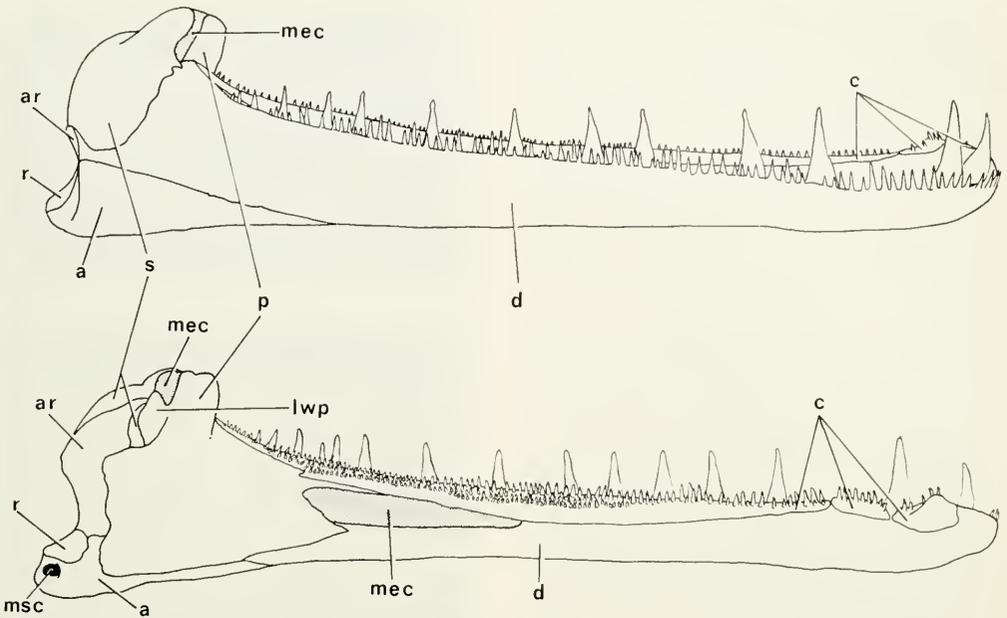


FIG. 7.—Lower jaw of *Atractosteus spatula* (AMNH uncat.). Upper, lateral view; lower, medial view. a, angular; ar, articular; c, coronoid; d, dentary; lwp, lateral wing of prearticular; mec, Meckel's cartilage; msc, mandibular sensory canal; p, prearticular; r, retroarticular; s, surangular.

hyomandibular can be identified) and Recent sharks, the ramus hyomandibularis VII passes the hyomandibular laterally and then branches. In rhipidistian sarcopterygians (*Eusthenopteron*, *Megalichthyes*, and other osteolepiforms and porolepiforms where the condition is known; Jarvik, 1954) and in coelacanth (*Nesides*, Jarvik, 1954; *Latimeria*, Millot and Anthony, 1958, 1965) the orientation of the ramus hyomandibularis VII to the hyomandibular is similar to actinopterygians, but the mandibular and hyoid branches apparently fork before penetrating the hyomandibular. The significance of the similarity between dipnoans and Recent sharks is obscure. *Polypterus* has the branching of the ramus hyomandibularis VII before the hyomandibular, like rhipidistians, but only the hyoid branch penetrates the hyomandibular whereas the mandibular branch curves in front of the hyomandibular (Goodrich, 1930, Fig. 446).

The structure of the lower jaw of actinopterygians has recently been stud-

ied by Nelson (1973b). He considered the presence of discrete articular, retroarticular and mentomeckelian endochondral ossifications and discrete prearticular and surangular dermal ossifications unfused with endochondral elements or themselves to be plesiomorphous characteristics of actinopterygians. The ossifications of the lower jaw of gars is shown in Fig. 7. Nelson (1973b) stated that a mentomeckelian is present as a separate ossification in *Amia* and is present and fused to the dentary in teleosts. Citing Starks (1916), Nelson mentioned the bone in large sturgeons. It is also present in *Pteronisculus* (Nelson, 1942), *Latimeria*, and *Polypterus* (Nelson 1973b). The absence of a mentomeckelian may be a synapomorphy of gars.

Chondrosteans, gars, and *Amia* have unfused, discrete articular and retroarticular ossifications. In chondrosteans and *Amia* the surangular and retroarticular are separated by an unrestricted mass of Meckel's cartilage, whereas in gars these bones are in contact. Teleosts

lack a surangular. Gars differ from other actinopterygians in having a lateral wing (lwp, Fig. 7) on the prearticular which restricts Meckel's cartilage and articulates with the surangular. The ventral surface of the lateral wing of the prearticular forms the dorsal roof of the cavity that houses the insertion of the adductor mandibular muscle. The prearticular and surangular meet above to produce a coronoid process. The dentary is long, reflecting the general lengthening of the skull. In dried preparations, the Meckelian groove runs one-third to one-half of the length of the dentary. Coronoids cap the dentary medially and support an outer row of small teeth and an inner row of large teeth. The mandibular sensory canal penetrates the angular and runs the length of the dentary (msc, Fig. 7; Allis, 1905).

The development and structure of the gar neurocranium has been studied by Veit (1907, 1911, 1927), Mayhew (1924), Hammarberg (1937), and De Beer (1937). Rayner (1948) compared the neurocranial ossifications of gars with those of semionotids and pointed out the similarities between the neurocranium of gars and *Lepidotes*. Her conclusions have formed the major basis for considering gars to be semionotids. An extensive study of the neurocranium of actinopterygians including gars by Patterson (1975) summarized earlier pertinent data and added new information on the structure of the neurocranium of phylogenetically important taxa. The ossifications of the neurocranium of *Lepisosteus oculatus* are shown in Fig. 8.

Patterson (1975:566) concluded that a hypothesis of loss of neurocranial ossifications is preferable to one of fragmentation or gain of neurocranial ossification centers. Further, he concluded that the palaeoniscoid *Perleidus* displays the primitive actinopterygian pattern. Table 1 is a summary of the ossification centers present in major groups of actinopterygians. The primitive pattern of *Perleidus* is most closely approximated by

those of parasemionotids and pholidophorids. Following this hypothesis gars and *Lepidotes* are more apomorphic than halecomorphs and teleosts. Both have lost the endochondral intercalar, the opisthotic, and (following Patterson, 1975) the "epioccipitals." The gars differ from *Lepidotes* in that gars have also lost the basisphenoid. The endochondral intercalar has been lost within both the Halecomorphii (amiids) and the Teleostei (pholidophorids, leptolepids and more derived groups) but the dermal intercalar is found in all halecostomes (Patterson, 1975). The opisthotic has been lost within the Teleostei and Amiidae. Further, the amiids have lost the pterotic (following Patterson, 1975). The loss of both the opisthotic and endochondral intercalar is, therefore, not unique to gars and *Lepidotes* within the Actinopterygii; both have been lost at least twice within other groups.

To consider these losses as synapomorphies uniting gars and *Lepidotes* into a single group, is, at the least, a weak hypothesis. Such a hypothesis is refuted by several other characters uniting *Lepidotes* to halecomorphs and teleosts. To consider these losses as plesiomorphous of Neopterygii would be unparsimonious in view of the similarities between parasemionotids, pholidophorids, and *Perleidus*. The adoption of this hypothesis would require the independent acquisition of several ossification centers in halecostomes and paleoniscoids, or the loss of ossification centers in the ancestor of neopterygians followed by a re-acquisition in two lineages and a loss within each lineage independently. While such hypotheses are possible, it is more parsimonious to consider the losses by gars and *Lepidotes* to be independent losses and therefore nonhomologous.

Gars have no anterior myodomes. The anterior myodomes are found in a number of chondrosteans, parasemionotids, *Dapedium*, caturids, and amiids (Patterson, 1975:515-516). Patterson

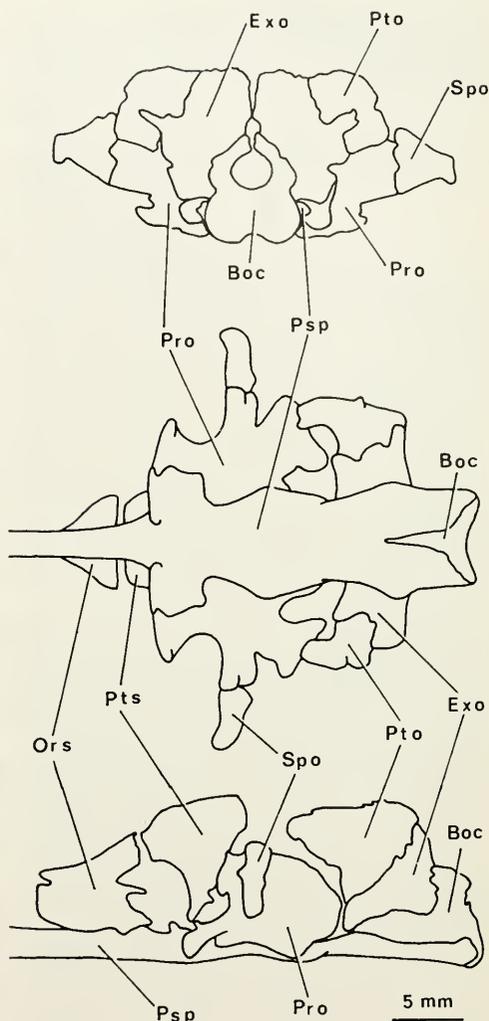
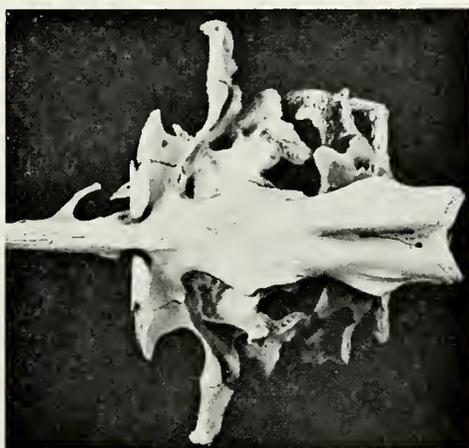
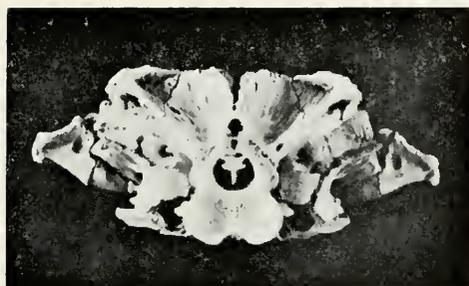


FIG. 8.—Neurocranial ossifications of *Lepisosteus oculatus* (LACM 33914-2). Top, posterior view; middle, ventral view; bottom, lateral view. Boc, basioccipital; Exo, exoccipital; Ors, orbitosphenoid; Pro, prootic; Psp, parasphenoid; Pto, pterotic; Pts, pterosphenic; Spo, sphenotic.

considered the gar condition secondary, and thus a synapomorphic character. Gars share with *Polypterus* and most primitive palaeoniscoids a transverse canal in the otic region, a characteristic Patterson (1973:254) thought precluded gars having secondarily lost a posterior myodome. Thus, Patterson reasoned that the large posterior myodome of *Amia* and teleosts is a synapomorphy of halecostomes.

Patterson (1973:253-254) stated that the basiptyergoid process of gars is in-

termediate between the condition in chondrosteans, where the process is entirely endochondral (i.e., via the prootic), and the derived condition in teleosts, where it is entirely dermal (lateral wings of the parasphenoid).

#### THE HYOID AND VISCERAL ARCHES

*Hyoid arch.*—The hyoid arch of gars consists of paired endodermal hypohyals, anterior and posterior ceratohyals, interhyals, and dermal paired primary basi-

TABLE 1.—Neurocranial Ossifications in seven groups of actinopterygian fishes.<sup>1</sup>

| Bone                  | T a x o n            |      |                    |                 |             |                |             |
|-----------------------|----------------------|------|--------------------|-----------------|-------------|----------------|-------------|
|                       | <i>Ptereleutidus</i> | gars | <i>Lepidotates</i> | parasemionotids | <i>Amia</i> | pholidophorids | leptolepids |
| Basioccipital .....   | X                    | X    | X                  | X               | X           | X              | X           |
| Exoccipital .....     | X                    | X    | X                  | X               | X           | X              | X           |
| Epioccipital .....    | X                    |      |                    | X               | X           | X              | X           |
| Supraoccipital .....  | ?                    |      |                    |                 |             | X              | X           |
| Derm-intercalar ..... |                      |      |                    | X               | X           | X              | X           |
| Endo-intercalar ..... |                      | X    |                    | X               |             | X              |             |
| Opisthotic .....      | X                    |      |                    | X               |             | X              |             |
| Pterotic .....        | X                    | X    | X                  | X               |             | X              | X           |
| Prootic .....         | X                    | X    | X                  | X               | X           | X              | X           |
| Basisphenoid .....    | X                    | X    | X                  | X               | X           | X              | X           |
| Sphenotic .....       | X                    | X    | X                  | X               | X           | X              | X           |
| Orbitosphenoid .....  | X                    | X    | X                  | ?               | X           | X              | X           |

<sup>1</sup> Patterson (1973).

hyal toothplates and branchiostegals (Fig. 9). Gars, like amiids and chondrosteans, lack the basihyal of teleosts (Wijlke, 1882; Veit, 1911; Hammarberg, 1937; Nelson, 1969a). A basihyal is hypothesized here to be a synapomorphy of teleosts, and may be derived from anterior prolongation of the first basibranchial copula (Nelson, 1969a).

The hypohyals of gars are rectangular and connected by connective tissue

to the basihyal toothplates of the spatulate "tongue." The anterior ceratohyal is long and uncompressed, whereas that of halecostomes is laterally compressed. The posterior ceratohyal is bent upward at a right angle to the vertical plane of the arch, articulating with the anterior ceratohyal, the interhyal, and the preopercular. The interhyal is usually unossified and connects the hyoid arch with the skull at the junction of the symplectic and hyomandibular cartilages. Three branchiostegals are present (McAllister, 1968). Two branchiostegals articulate with the posterior ceratohyal and one articulates with the anterior ceratohyal, or occasionally at the junction of the two ceratohyals. That the most posterior branchiostegal is the homologue of the interopercular of halecostomes (De Beer, 1937) has been rejected by McAllister (1968). What, if any, phylogenetic significance can be attached to the small number of branchiostegals in gars is not clear because many groups have apparently reduced the number of branchiostegals independently (see McAllister, 1968, for discussion).

Gars are the only known actinopterygian group having a long series of paired primary basihyal toothplates associated with a long spatulate "tongue" (Nelson, 1969a). These toothplates make up the

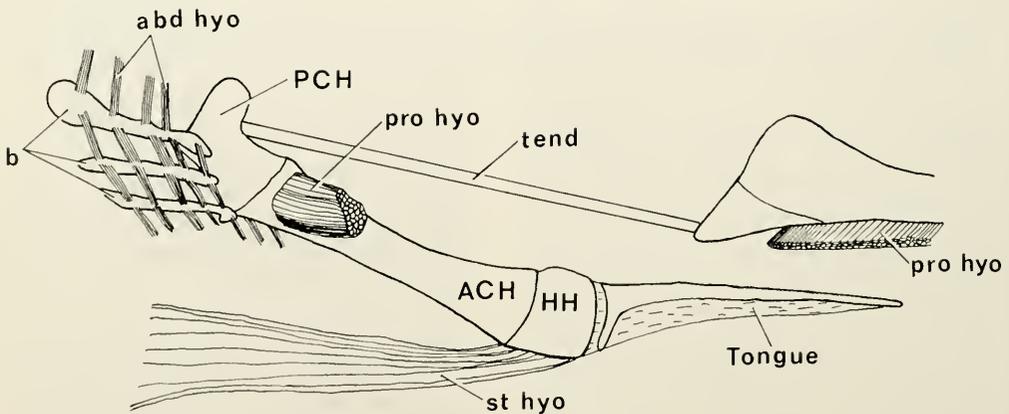


FIG. 9.—Diagrammatic lateral view of the hyoid apparatus of a gar. ACH, anterior ceratohyal; abd hyo, abductor hyoides; b, branchiostegal; HH, hypohyal; PCH, posterior ceratohyal; pro hyo, protractor hyoides; st hyo, sternohyoides; tend, tendon.

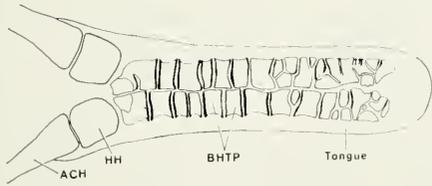


FIG. 10.—“Tongue” of *Lepisosteus osseus* (AMNH 509). Dorsal view. ACH, anterior ceratohyal; BHTP, basihyal tooth plates; HH, hypohyal.

dorsal surface of the tongue, articulate with each other and are supported by the dense connective tissue underlying them (Fig. 10). Whereas the presence of basihyal toothplates is probably plesiomorphous for actinopterygians, the number and arrangement of the basihyal toothplates in gars is hypothesized as synapomorphous.

The hyoid arch is connected to the cleithrum by the sternohyoids, which originate on the medial wing of the cleithrum and insert on the hypohyals (st hyo, Fig. 9). The protractor hyoideus originates on the posterior half of the anterior ceratohyal and inserts along the lower edge of the posterior half of the lower jaw (pro hyo, Fig. 9). Gars have a ligament, not reported in other fishes, which connects the posterior ceratohyal with the retroarticular of the lower jaw (tend, Fig. 9). This ligament does not seem to be the functional analogue of the tendon of halecostomes that connects the interopercular with the lower jaw and which has a respiratory function (Schaeffer and Rosen, 1961). In gars the ligament may provide the functional equivalent of the halecostome protractor hyoideus. In halecostomes this muscle is well developed and inserts on the lower jaw symphysis, whereas in gars it is weak, not inserted at the symphysis, and is probably not capable of coordinating the movement of the lower jaw and hyoid arch. The ligament of gars, however, seems capable of depressing the lower jaw upon contraction of the sternohyoideus. It could also function in keep-

ing the lower jaws in line and working in concert with the hyoid arch. Thus, I hypothesize that the ceratohyal-retroarticular ligament of gars has a primary feeding function in contrast to the interopercular-retroarticular tendon of halecostomes which has a primarily respiratory function.

The hyoid arch is connected to the opercular series via the abductor hyoideus. This muscle consists of a series of muscle sheets running between the branchiostegals and inserting on the opercular bones. Finally, the hyoid arch is connected with the anterior end of the basibranchial copulae by articulation via the hypobranchials and via a tendon running from the anterior ceratohyal to the first hypobranchial.

*Visceral arches.*—Various morphological structures of the visceral arches of gars have been cited as evidence for a monophyletic Holostei (Nelson, 1969a) and against a monophyletic Holostei (Patterson, 1973). Gars, like other actinopterygians, have five paired arches united ventrally by a series of basibranchial copulae.

The basibranchial copulae of gars have been described and compared with those of other fishes by Nelson (1969a). Gars are similar to halecostomes in having four copulae (Fig. 11a, b). The “Gogo palaeoniscoids” have a single basibranchial, a condition Gardiner (1973) considered plesiomorphic for the Actinopterygii. Gardiner (1973) stated that this plesiomorphic condition is retained in *Polypterus* (Fig. 11c). In *Acipenser* there are three ossifications in a single basibranchial copula (Wijhe, 1882; Gardiner, 1973), whereas in *Polyodon* (Fig. 11d) there are three copulae (Nelson, 1969a), a condition similar in the palaeoniscoids *Birgeria* (Stensiö, 1921) and *Pteronisculus* (Nielsen, 1942). Nelson (1969a) and Gardiner (1973) reviewed the number of copula in other teleostomes. Four copulae, then, seem to be synapomorphous for the Neopterygii.

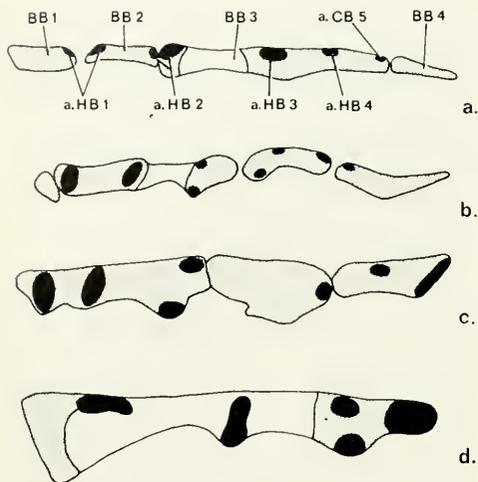


FIG. 11.—Lateral view of the basibranchial copulae of four actinopterygians, after Nelson, 1969a. a. *Lepisosteus platostomus*; b. *Amia calva*; c. *Polyodon spatula*; d. *Polypterus* sp. Cartilage stippled, hypobranchial articular surfaces black, bone unstippled. a. CB5, articular surface of ceratobranchial 5; a. HB 1-4, articular surfaces of hypobranchials 1-4; BB1-4, basibranchials 1-4.

The position of the articulation of the hypobranchials to the basibranchial copulae also varies between actinopterygian groups. In gars (Fig. 11a) hypobranchial 1 articulates at the junction of the basibranchials 1 and 2, hypobranchial 2 articulates at the junction of basibranchials 2 and 3, hypobranchials 3 and 4 and ceratobranchial 5 articulate with basibranchial 3, and basibranchial 4 supports no paired arch elements (Nelson, 1969a). In *Pteronisculus*, basibranchial 1 supports no paired arch elements and was termed the basihyal by Nielsen (1942). *Polyodon* and *Amia* (Figs. 11d, b) are similar to each other in having hypobranchials 1 and 2 articulating with basibranchial 1. In *Polyodon*, hypobranchials 1 to 3 all articulate with basibranchial 1 and if this basibranchial is homologous to basibranchials 1 and 2 in *Pteronisculus*, then they have a similarity not present in neopterygians.

*Amia*, teleosts, and chondrosteans (where the condition is known) are similar in having the articular ends of hypo-

branchial 4 penetrated by the ventral aorta. Gars have hypobranchials that are not penetrated by the ventral aorta, a condition hypothesized here as apomorphic.

*Amia* and gars have a perichondral ossification on the copula between arches 2 and 3 (Fig. 11a, b). Gars occasionally have two other ossifications (Patterson, 1973). The significance of this similarity is lessened by the observations that (1) the ossifications are not found on the same copula, being found on basibranchial 2 in *Amia* and basibranchial 3 in gars, and (2) perichondral ossifications of basibranchials are found in palaeoniscids (Stensiö, 1921; Nielsen, 1942; Gardiner, 1973) and may be primitive for actinopterygians or derived several times independently. These observations weaken Nelson's (1969a) hypothesis that this ossification is a synapomorphy uniting *Amia* and gars.

Gars are similar to chondrosteans and *Amia* in having a separate fourth hypobranchial, which teleosts lack (Nelson, 1969a). The condition in teleosts is hypothesized to be apomorphic relative to those of other actinopterygians.

In gars the hypobranchials and ceratobranchials are simple rod-like structures. There are four epibranchials. The first two epibranchials have uncinete processes (UP, Fig. 12b). Chondrosteans lack uncinete processes (Fig. 12a), whereas *Amia* and teleosts have uncinete processes on the third epibranchial, as well as on the first two epibranchials (Fig. 12c). In *Amia* the third uncinete process is not prominent and is cartilaginous, whereas in teleosts it is well developed and ossified. I hypothesize that the lack of uncinete processes, the condition of chondrosteans, is plesiomorphous for actinopterygians. Gars, *Amia*, and teleosts share the synapomorphy of having uncinete processes. Gars have the relatively plesiomorphous condition of two uncinete processes relative to the three possessed by halecostomes.

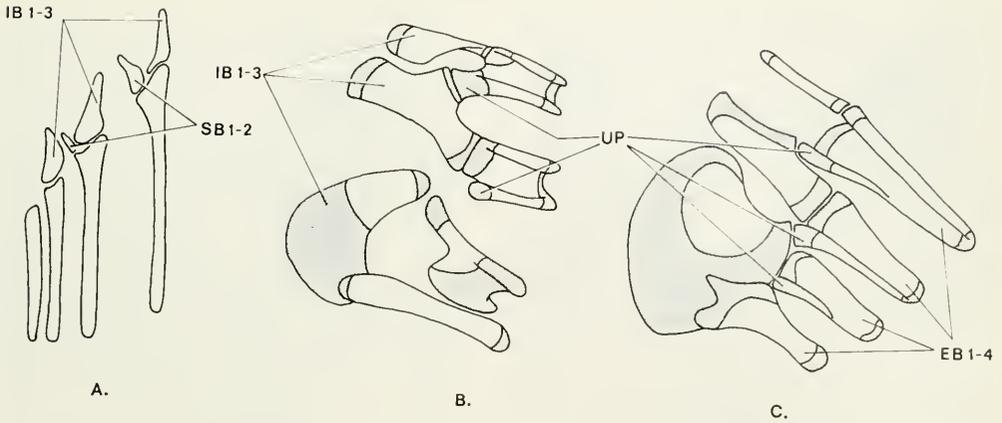


FIG. 12.—Dorsal view of the upper gill arch elements of: (A) “*Gogo palaeoniscoid*,” after Gardiner, 1973, (B) *Atractosteus tropicus*; and (C) *Amia calva*. Cartilage stippled, bone unstippled. Suprapharyngobranchials omitted in B and C. EB1-3 or 4, epibranchials 1-3, 4; IB1-3, infrapharyngobranchials 1-3; SB1-2, suprapharyngobranchials 1-2; UP, uncinat process.

Gars, *Amia*, and chondrosteans lack a fourth infrapharyngobranchial (Fig. 12), whereas teleosts have this structure. Presence of a fourth infrapharyngobranchial was considered plesiomorphous by Nelson (1969a) but apomorphous by Patterson (1973). Nelson’s (1969a) conjecture was based on the observation that elasmobranchs and acanthodians have a fourth infrapharyngobranchial. Patterson’s (1973) conjecture was based on the observation that all actinopterygians except teleosts lack a fourth infrapharyngobranchial. Acceptance of Nelson’s (1969a) hypothesis would require acceptance of a monophyletic group composed of chondrosteans, gars, and *Amia*. This hypothesis is incongruent with hypotheses based on other characters. I accept Patterson’s (1973) hypothesis and suggest that the fourth infrapharyngobranchial of teleosts originated as a subdivision of the third infrapharyngobranchial. Thus, the fourth infrapharyngobranchial of teleosts is hypothesized to be not homologous with the fourth infrapharyngobranchial of elasmobranchs and acanthodians.

Chondrosteans have infrapharyngobranchials that are posteriorly supported by the epibranchials (Fig. 12a; Gardiner, 1973; Nielsen, 1942). In gars, *Amia*, and

teleosts, the infrapharyngobranchials are laterally supported by the epibranchials (Fig. 12b, c). This change in orientation for support of the infrapharyngobranchials is hypothesized an apomorphy for neopterygians.

Neither gars nor chondrosteans have a fifth epibranchial. Allis (1897) figured a fifth epibranchial in *Amia* but Bertmar (1959) failed to find this structure. I have been unable to find a fifth epibranchial on 37-40 mm cleared and stained specimens of *Amia*. A “fifth epibranchial” is found in primitive teleosts as a small ball of cartilage, and Nelson (1969a) interpreted this character as a retained plesiomorphy. This hypothesis is weakened by two observations—it is absent in other actinopterygian groups, and additional balls of cartilage are found in higher teleosts (Rosen, pers. comm.). It is possible that the “fifth epibranchial” is simply another of these balls of cartilage and thus an apomorphy found in certain teleosts.

*Dermal Components of the Arches.*—The dermal ossifications associated with the endoskeletal visceral skeleton may be divided conveniently into dermal toothplates and gill rakers, these rakers being modified toothplates. Nelson (1969a, 1970b) hypothesized that the

primitive condition for gnathostomes consists of a well developed dermal arch skeleton composed of separate toothplates covering the buccal cavity from the jaw margin to the pharyngo-esophageal border. Apomorphous conditions usually involve reductions of dermal elements and have occurred in both elasmobranchs (Nelson, 1970b) and osteichthyans (Nelson, 1969a). Nelson (1969a, 1970b) hypothesized the plesiomorphous condition for osteichthyans to consist of six rows of dermal elements: (1) lateral plates, (2) lateral gill rakers, (3) two rows of medial toothplates, (4) medial gill rakers, and (5) inner plates. *Lati-meria* has retained the primitive osteichthyan features (Nelson, 1969a). Among chondrosteans, *Pteronisculus* has several rows of toothplates associated with each arch (Nielsen, 1942). Living chondrosteans have reduced their dermal plates to a single row of medial toothplates on the first hypobranchials (Nelson, 1969a). Gars have reduced their medial toothplates to a greater degree than *Amia* or teleosts. Gars have a single row of medial toothplates on hypobranchials 1, 2, and 3, ceratobranchials 2, 3, and 4, and on epibranchial 1. Gars have lost medial toothplates on ceratobranchial 1. Two rows of medial toothplates (the plesiomorphous condition) are found on hypobranchial 4 and infrapharyngobranchial 2, while several rows of toothplates are found on ceratobranchial 5 and infrapharyngobranchial 3. *Amia* and primitive teleosts retain the plesiomorphous number of rows of medial toothplates on each of the lower arches. *Amia* differs from gars and teleosts in lacking the inner and lateral plates.

Nelson (1969a) concluded that neopterygians are the only osteichthyan fishes with significantly developed upper pharyngeal dentition. He hypothesized that the organization of the toothplates on the third infrapharyngobranchial and the lack of a fourth infrapharyngobranchial were synapomorphies uniting *Amia* and gars. This hypothesis rests on

two conjectures: (1) that the fourth infrapharyngobranchial is plesiomorphous, a conjecture refuted above, and (2) that the several rows of teeth on the third infrapharyngobranchial of holosteans are derived from two or more arches (Nelson, 1969a, suggested that dermal elements of arches 3, 4, and possibly 5 are involved). Conjecture two seems to rest on the assumption that the toothplates on the third infrapharyngobranchial are homologous with only the medial toothplates of the lower arch elements. But there are only five or six rows of toothplates on infrapharyngobranchial 3 of gars, and it is possible that these are homologous with the entire six rows of dermal elements present primitively on the lower arches. I offer this conjecture as an alternative hypothesis and suggest that the two upper patches of teleosts arose from the simple subdivision of the primitively single third infrapharyngobranchial.

*Visceral arch muscles.*—The visceral arch musculature of actinopterygians has been used to corroborate a hypothesis of a monophyletic Holostei (Nelson, 1969a). Other groups in which this character complex has been used successfully to demonstrate relationships include the eels (Nelson, 1966), the neoteleosts (Rosen, 1973), and the tetradontiforms (Winterbottom, 1972).

*Dorsal arch musculature.*—The primitive dorsal arch musculature of actinopterygians is hypothesized here to be similar to that seen in living *Polyodon* and *Acipenser*. In these genera there is a series of levator muscles running from the epibranchials to the skull roof and two medial muscle layers; a longitudinal layer lining the buccal cavity overlain by a circular layer. Both layers are undifferentiated from the same muscle layers lining the esophagus. Gars, *Amia* and teleosts differ from chondrosteans in having discrete muscles derived from the circular muscle layer. These muscles include the transverse dorsalis and oblique dorsalis (Fig. 13). I conclude that the

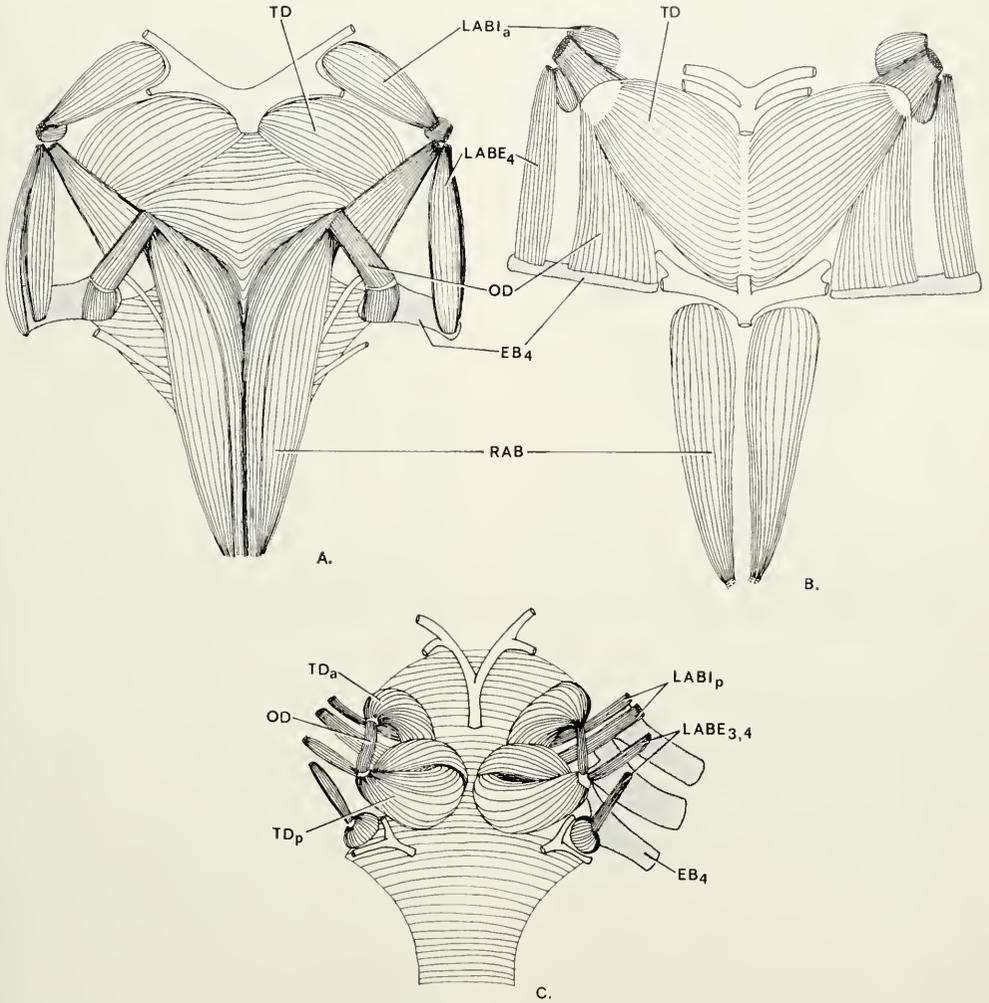


FIG. 13.—Dorsal view of the upper gill arches of (A) *Amia calva*; (B) *Lepisosteus oculatus*; and (C) *Albula vulpes*. Semidiagrammatic; bone stippled, muscles lined, dorsal aorta unstippled. EB 3, 4, epibranchial 3, 4; LABE 3, 4, levator arcus branchialis exterior 3 and 4; LABI a and p, levator arcus branchialis interior, anterior and posterior; OD, oblique dorsalis; RA, retractor arcus branchialis; TD, a, p, transverse dorsalis, anterior, posterior.

presence of such muscles is an apomorphy of neopterygians.

Retractor muscles are found in all three neopterygian groups. Retractors move the posterior infrapharyngobranchial(s) and originate on the vertebrae. Teleost retractors are not found in all lower teleosts (Nelson, 1966, 1967; Rosen, 1973) and are derived from the inner longitudinal muscle layer (Rosen, 1973). The retractors of gars and *Amia* are derived from the outer circular muscular

layer (pers. observ.). Dietz (1912, 1914, 1921), Nelson (1966, 1967), and Rosen (1973) concluded that the retractors of teleosts are not homologous with the holostean retractors. Rosen (1973) pointed out that teleost retractors have arisen a number of times within the Teleostei.

Nelson (1969a) concluded that the retractors of amiids and gars are synapomorphic. Patterson (1973) suggested that multiple independent development of retractors in teleosts weakens Nelson's

(1969a) hypothesis. In support of Nelson's argument are the observations that the retractors of both gars and *Amia* originate on the vertebral column and insert on the third infrapharyngobranchial, and that they have a similar embryological development, at least to the point that both are derived from the same muscle layer. Embryological studies indicate that the retractors of both groups are derived from either the esophageal sphincter (Edgeworth, 1911, 1928) or from a posterior muscle mass independent of the esophageal sphincter (Edgeworth, 1935).

In refutation of Nelson's (1969a) hypothesis are the following observations. The retractors of gars (Fig. 13a) originate separately, one on each side of the vertebral column on the third, fourth, and occasionally fifth vertebrae. They remain separate muscles and insert separately on the posterior edge of the third infrapharyngobranchial. They do not share muscle fibers with the transverse dorsalis but do share muscle fibers with the underlying circular muscle layer of the esophagus. Each transverse dorsalis of gars originates separately along the midline connective tissue and dorsal surface of the third infrapharyngobranchial and inserts in conjunction with the oblique dorsalis on the anterolateral cartilaginous tip of the ossified lateral arm of the third infrapharyngobranchial. In *Amia calva* (Fig. 13b), the retractors originate as a single muscle on the vertebral column, separating anteriorly into the two masses. They insert on the dorsal surface of the third infrapharyngobranchial and are confluent with the transverse dorsali. The transverse dorsali do not insert in conjunction with the oblique dorsali; rather, the retractors insert with the oblique dorsali, and the transverse dorsali are found anterior to this insertion. Finally, the retractors of *Amia* do not share muscle fibers with the circular muscle layer of the esophagus. Lower teleosts, for example *Albula* (Fig. 13c), have no retractors. But,

the posterior transverse dorsali have the same origin and insertion and the same topographic relationship with the oblique dorsali of the fourth epibranchial as gars. And, the insertion of the posterior transverse dorsalis and the oblique dorsalis of the fourth epibranchial of *Albula* is the same as the insertion of the retractor and the oblique dorsalis of the fourth epibranchial of *Amia calva*.

I interpret the retractor of *Amia* as a derivative of the transverse dorsalis and not as the homologue of the retractor of gars. This interpretation would explain three observations: (1) the association of the oblique dorsalis of the fourth epibranchial and retractor in *Amia*, (2) the sharing of fibers of the circular muscle layer and retractor of gars and the non-sharing of circular fibers and the retractors of *Amia*, and (3) the confluence of the transverse dorsali and retractors in *Amia* and the separation of these muscles in gars. I conclude that the retractors of *Amia* and gars are independently derived and therefore not evidence for a relationship between the two groups.

*Ventral arch musculature.*—The ventral gill arch muscles of osteichthyans have been studied by Edgeworth (1928, 1935) and Nelson (1967). Nelson (1967) hypothesized that oblique ventralis muscles are associated with each hypobranchial and ceratobranchial as a primitive condition for osteichthyans and that loss of a hypobranchial is correlated with the presence of a transverse ventralis muscle on the arch. Chondrosteans lack transverse ventralis muscles but have a pair of oblique dorsali on each arch. Gars and *Amia* differ from chondrosteans and are similar to teleosts in having a transverse ventralis muscle on the fourth arch (Fig. 14a, b). Gars and *Amia* differ from teleosts in retaining a fourth hypobranchial and a fourth oblique ventralis which shares fibers with the transverse ventralis. I hypothesize that the presence of a transverse ventralis is a synapomorphy of neopterygians, that the

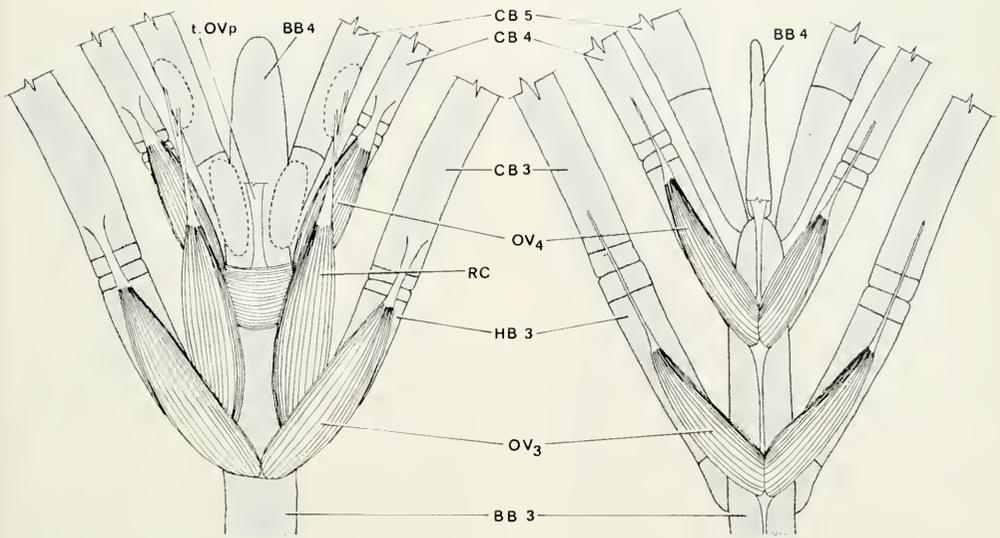


FIG. 14.—Ventral view of the posterior gill arches of *Amia calva* (left) and *Atractosteus spatula* (right). Semidiagrammatic; bone and cartilage stippled, muscles lined, tendons white. BB 3-4, basibranchials 3-4; CB 3-5, ceratobranchials 3-5; HB3, hypobranchial 3; OV<sub>3</sub>-OV<sub>4</sub>, oblique ventralis 3 and 4; RC, rectus communis; t. OVp, tendon of oblique ventralis posterior.

retention of a fourth pair of oblique ventralis muscles and the fourth hypobranchials are plesiomorphies, and well developed fourth oblique ventralis are synapomorphies of teleosts.

*Amia* and teleosts differ from gars in having a pair of rectus communis muscles (Fig. 14b, c). These muscles originate at the base of the third hypobranchials and insert via a tendon on either the fourth ceratobranchial (teleosts) or the fifth ceratobranchial (*Amia*). In both these groups of halecostomes the rectus communis is innervated by fourth arch nerve fibers and shares muscle fibers with the fourth transverse ventralis. Nelson (1967) suggested that the muscle was derived from the fourth transverse ventralis by forward growth. The presence of a rectus communis is hypothesized an apomorphy of halecostomes.

The ventral muscles of the fifth arch in actinopterygians are, like the dorsal muscles, derived from the outer circular muscle layer of the buccal and esophageal cavities. In the chondrosteans *Polyodon* and *Acipenser*, there are two

muscles, the transverse ventralis running between the fifth ceratobranchials and the coracobranchialis which originate on the midline connective tissue and insert on the coracoid of the pectoral girdle. In *Polyodon* the coracobranchialis is composed of many separate muscle bundles and is not attached to the basibranchial copula. This muscle in *Polyodon* is little differentiated from the transverse ventralis, which runs between the ceratobranchials immediately posterior to the coracobranchialis, and it is undifferentiated from the circular muscle layer of the esophagus. In *Acipenser* the coracobranchialis is better defined, originating at the midline as a pair of discrete muscles connected by a tendon to the basibranchial copulae and inserting on the coracoid of the pectoral girdle. The transverse ventralis, like that of *Polyodon*, originates on the midline connective tissue and inserts along the fifth ceratobranchials. In neopterygians the coracobranchialis does not originate on the midline connective tissue but on the lateral surfaces of the fifth cerato-

branchials. In *Amia* and gars the coracobrachialis inserts on the cleithrum whereas in *Elops* and *Salmo* it inserts on both the cleithrum and the coracoid (Jessen, 1972). The transverse ventralis of gars and *Amia* is essentially like that of chondrosteans except that it is better differentiated from the circular muscle layer of the esophagus (but it still shares fibers extensively). Teleosts are different. In *Elops* and *Albula*, the transverse ventralis no longer inserts on the fifth ceratobranchials but on the cleithrum via a tendon. The distribution of this character will have to be investigated in other teleosts before its significance can be assessed.

#### POSTCRANIAL SKELETON

*Dermal components of the pectoral girdle.*—The dermal pectoral girdle of gars includes the post-temporal, supra-cleithrum, and cleithrum (Fig. 15). The post-temporal articulates with the suprateremporals above and the pterotic medially and ventrally. The articular surface of the gar post-temporal is convex, allowing for a ball-and-socket-like articulation of the supra-cleithrum via the concave supra-cleithral articular surface. The post-temporal of gars is similar to those of chondrosteans and *Polypterus* in lacking a post-temporal process. *Amia* and teleosts have a post-temporal process that articulates with the dermo-intercalar (see figures in Jessen, 1972; pers. observ. of *Elops*, *Megalops*, *Albula*, *Chupea*, *Osteoglossum*, and *Salmo*). Patterson (pers. comm.) reports the process in at least some semionotids. The presence of a post-temporal process in halecostomes is hypothesized apomorphic relative to its absence in gars and chondrosteans. The mode of articulation between the post-temporal and supra-cleithrum in gars is unique and hypothesized apomorphic for that group.

The supra-cleithrum of gars has a supra-cleithral process that is connected to the basicranium via a ligament. *Polypterus* also has a supra-cleithral process

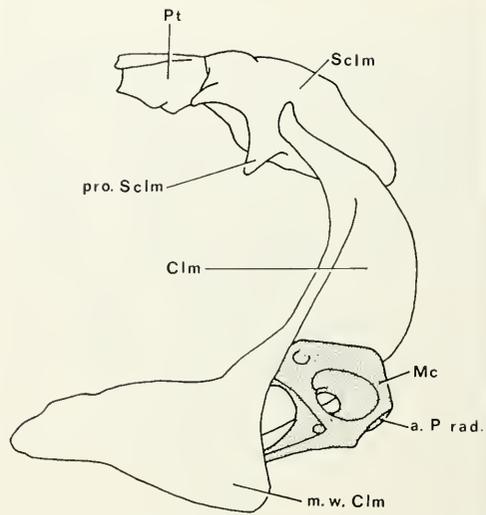


FIG. 15.—Medial view of the pectoral girdle and post-temporal of *Lepisosteus osseus*. Dermal bones unstippled, endoskeletal mesocorocoid stippled. A. P rad, articular surface of pectoral radials; Clm, cleithrum; Mc, mesocorocoid; m.w. Clm, medial wing of cleithrum; pro. Sclm, supra-cleithral process; Pt, post-temporal; Sclm, supra-cleithrum.

(Daget, 1950; Jessen, 1972), but Jessen (1972) reported that the process is connected via a ligament to the epaxial body muscles, not the basicranium. Such a process has not been reported in chondrosteans and there is little reason to conclude that the supra-cleithral processes of *Polypterus* and gars are homologous. I conclude that the process is apomorphic and independently derived in both groups.

The cleithrum of gars differs from that of other actinopterygians in having a well-developed medial wing (M.W. Cl, Fig. 15). This structure serves as the attachment area for the pectoral adductors, the ventral body musculature, and the sternohyoideus (Jessen, 1972). This structure is hypothesized apomorphic for gars. The cleithrum is connected to the supra-cleithrum via connective tissue and articulates with its opposite medially along the ventral edges of the cleithral wing. The cleithrum is connected to the vertebral column via Baudelot's ligament and to the visceral

arches via the coracobranchialis and sternohyoideus.

Gars, like *Amia* and teleosts (and all known fossil neopterygians), lack a clavicle. Attempts to homologize the small ossicles found on some gars (Jarvik, 1944) and the small flagellae of *Amia* with the clavicle of chondrosteans are not convincing and I hypothesize that the lack of a clavicle is a neopterygian synapomorphy.

*Endoskeletal pectoral girdle and Jessen's hypothesis of Actinopterygian relationships.*—The endoskeletal pectoral girdle of chondrosteans, gars, *Amia*, and teleosts has been studied in detail by Jessen (1972). His interpretation of the shoulder girdle of actinopterygians led him to hypothesize that holosteans have a fundamentally different endoskeletal structure than teleosts and chondrosteans. Thus, Jessen (1972, 1973) concluded that chondrosteans are the sister group of teleosts and that *Amia*, gars, and *Bergeria* are the sister group of all other actinopterygians.

Jessen's hypothesis rests on three characters hypothesized by him (Jessen, 1973) to be synapomorphies of gars and *Amia*. Two are shoulder girdle characters and one concerns the course of the spinal nerves (and will be discussed here for completeness).

- 1—The medial process of the scapular region of chondrosteans and teleosts is not homologous with a similar process in *Amia* and gars that Jessen termed the pontiform process.
- 2—Gars and *Amia* lack a coracoid region that teleosts and chondrosteans have.
- 3—The spinal nerves of gars and *Amia* penetrate the body musculature ventral to the transversely oriented pleural ribs, whereas in chondrosteans, teleosts, and all other gnathostomes the spinal nerves follow the inner side of the body musculature mesial to the pleural ribs.

Patterson (1973:259-260) outlined and discussed these points. He concluded that: character (1) is refuted by his suggestion that the differences in the upper endoskeletal girdle of gars and *Amia* could be accounted for by changes in the orientation and relative size of the parts, character (2) is refuted by demonstrating that gars have a coracoid canal of the same type as other actinopterygians and which marks the boundary between the scapular and coracoid regions of the endoskeletal girdle. Thus, the "anterior process of the middle region" (Jessen, 1972) is the homologue of the "anterior process of the coracoid region" (Patterson, 1973). Patterson (1973) concedes that the course of the spinal nerves is a significant similarity. I conclude from this that a hypothesis of synapomorphy concerning the course of the spinal nerves of *Amia* and gars cannot be refuted on morphological grounds, and therefore must be refuted on phylogenetic grounds, that is, by its incongruence with other hypothesized synapomorphies.

*Vertebrae.*—The structure and development of actinopterygian vertebrae have been reviewed by Schaeffer (1967a) and his analysis will serve for the developmental statements made below. The axial skeleton of all gnathostomes has, primitively, neural and haemal arches derived from sclerotomic mesenchyme at the position of the myosepta. Intercalaries are present in sarcopterygians (except *Neoceratodus*), chondrosteans, *Amia*, and perhaps gars (in a modified form), but intercalaries are absent in teleosts and *Polypterus*. Whether centra are a primitive neopterygian feature or not is not clear. All three neopterygian groups have centra, but in at least one primitive halecomorph centra are missing (Patterson, 1973). The centra of amiids and teleosts are amphicoelous whereas those of gars are opisthocelous (Fig. 16), a character unique among all actinopterygians except the blenny *Andamia* (Schaeffer,



FIG. 16.—Vertebra of *Atractosteus africanus* (MHNP N.29, length of ventral ridge 13mm).

1967a). The amphicoelous vertebrae of teleosts differ in development from those of *Amia*. In teleosts the centrum forms as a double ring, an inner ring calcifying in the fibrous sheath of the notochord (the chordacentrum) and an outer ring which ossifies later in the perichordal tube (the autocentrum) and later replaces the chordacentrum to form the definitive adult centrum. In *Amia* a thin layer of bone forms in the perichordal tube and this is rapidly overlain by cancellous bone derived from the sclerotomic mesenchyme. Gars show a third pattern. Cartilaginous rings develop intrasegmentally in the perichordal tube.

These rings increase in size and detach from the arches. Before ossification the rings constrict the notochord and each is split by a transverse canal which forms the opisthocoelous joint. This split is an intrasegmental rather than intersegmental subdivision of the perichordal tube and the notochord. Because of the differences in development and adult structure, I hypothesize that the opisthocoelous vertebrae of gars are apomorphic for that group.

*Caudal skeleton.*—Gars have numerous hypurals, ural centra, and epurals. The neural arches of the ural centra are not modified into uroneurals and remain paired. The first ural centrum is usually fused to the last preural centrum and thus a compound centrum supports the parhypural and first hypural. Occasionally a second and even third hypural will be associated with the fused centrum.

Patterson (1973) reviewed the caudal fin structure of neopterygians and concluded that: (1) the presence of uroneurals in teleosts is apomorphic relative to the undifferentiated neural spines of *Amia* and gars; (2) the presence of median neural spines in *Amia* is intermediate between teleosts (with median uroneurals = neural spines) and gars; (3) numerous ural centra, hypurals and epurals are a primitive feature of actinopterygians; (4) the fused hypural-ural centra in *Amia* is apomorphic relative to the unfused condition in teleosts and gars; (5) the one-to-one correspondence between the middle hypurals and fin rays of gars and all of the fin rays and hypurals of *Amia* may have been derived independently; (6) epaxial fin rays developed independently in recent teleosts and *Amia*; (7) the absence of radials at the tips of the last few haemal spines of *Amia* is apomorphic relative to their presence in gars and teleosts, and (8) that two hypurals articulating with a first ural centrum is found in gars as an individual variation. I can find no reason to reject Patterson's (1973) first seven points, but the condition of the

fused first ural and last preural centra and their support of the parhypural and first hypural may be an apomorphy for gars and not a matter of individual variation.

#### SUMMARY HYPOTHESES OF ACTINOPTERYGIAN RELATIONSHIPS

The synapomorphies discussed above are organized below in five phylogenetic hypotheses (Figs. 17-19). In each case, the least rejected hypothesis is presented first and is followed by the alternative hypothesis which has corroborating instances based on characters that cannot be refuted as synapomorphies on morphological grounds. Alternate hypotheses for which no corroborating instances were found are not presented (for example, Jessen's, 1972, hypothesis). Characters discussed by Patterson (1973) as almost unique parallelisms among *Amia* and recent teleosts are not included because Patterson's (1975) analysis of fossil halecostomes indicates that these characters are nonhomologous, thus eliminating them from considerations of relationship.

Fig. 17a is the least rejected hypothesis of recent actinopterygian relationships based on the assumption followed throughout the analysis that chondrosteans are a monophyletic group. This is the same hypothesis accepted by Patterson (1973) and, eliminating fossil groups, by Westoll (1944), Gardiner (1960, 1963, 1967), and others. The monophyly of halecostomes is corroborated by 13 synapomorphies (characters 1-13, Fig. 17a). The monophyly of neopterygians is corroborated by 7 synapomorphies (characters 14-20, Fig. 17a). This hypothesis is not compatible with two characters, similarities of the endoskeletal pectoral girdle and the course of the spinal nerves of *Amia* and gars (Jessen 1972, and 1973, respectively). Both of these characters corroborate a hypothesis of monophyly of the Recent

Holostei and are incorporated into the alternate hypothesis of relationship shown in Fig. 17b. This hypothesis was forwarded by Nelson (1969a). Nelson (1969a) based the hypothesis on gill arch characters, which, as discussed above, are open to alternate interpretations incorporated in the first hypothesis (Fig. 17a).

Fig. 18a and b summarizes alternate hypotheses of relationships of the fossil semionotid genus *Lepidotes*. Fig. 18a summarizes the corroborating observations forwarded by Patterson (1973) that *Lepidotes* is a halecostome. Fig. 18b summarizes the corroborating observations discussed by Patterson (1975) for Rayner's (1941, 1948) hypothesis that *Lepidotes* is more closely related to the Ginglymodi than to halecostomes. *Lepidotes* shares five synapomorphies (characters 1-5, Fig. 18a) with halecostomes and only two (characters 6, 7, Fig. 18b) with ginglymods. Both of these characters are reduction characters that have arisen independently within both the Halecomorphi (amiids) and the Teleostei (see Patterson, 1975 and discussion above).

Fig. 19 summarizes the synapomorphies uniting the ginglymod genera *Lepisosteus* and *Atractosteus* (characters 1-27). No alternative hypothesis has been forwarded which refutes this hypothesis.

#### SUMMARY

Gars form a monophyletic group, the Ginglymodi. Gars are the sister group of the Halecostomi, a group composed of "semionotids" (*Lepidotes*, etc., a paraphyletic or polyphyletic assemblage; Patterson, 1973) the Halecomorphi (amiids and their fossil relatives the parasemionotids, Patterson, 1973), and the Teleostei. Gars and Halecostomes form the monophyletic group Neopterygii and this group is the sister group of the Chondrostei.

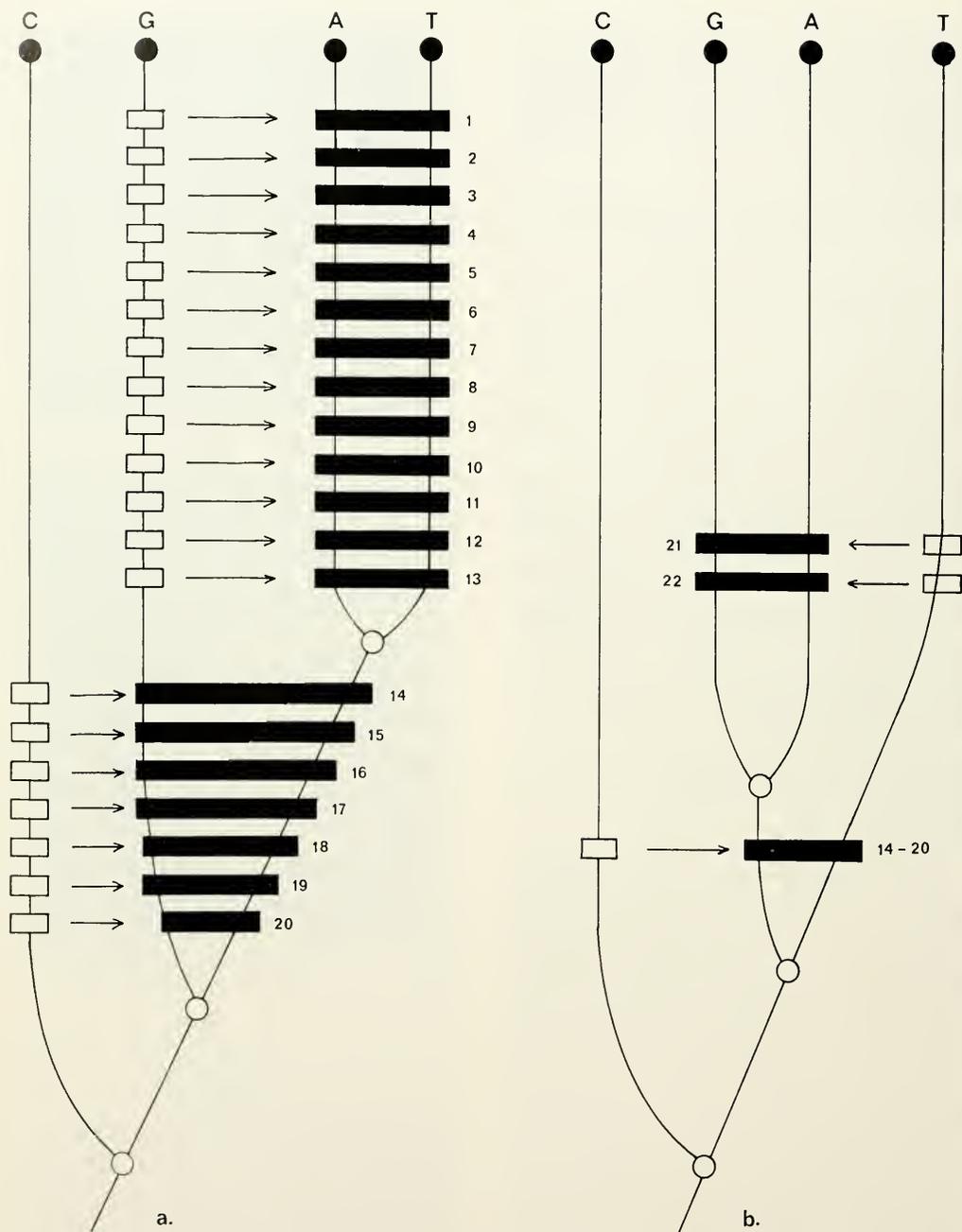


FIG. 17.—Alternate hypotheses of the relationships of chondrosteans (C), gars (G), amiids (A), and teleosts (T). (a) Least refuted hypothesis; (b) alternate hypothesis with corroborating characters. Synapomorphies (black rectangles) connecting taxa are: (1) a dermal intercalar; (2) a posterior myodome; (3) a supramaxilla; (4) a post-temporal process; (5) loss of internarial commissure; (6) an endochondral rostral; (7) maxilla with internal articulatory head; (8) a single supratemporal on each side of the midline; (9) circumorbital ring incomplete; (10) an interopercular; (11) uncinatc process on third infrapharyngobranchial; (12) a rectus communis muscle; (13) median neural spines in caudal region; (14) basipterygoid process entirely composed of parasphenoid; (15) a postnarial commissure between the supra- and infraorbital canals; (16) no clavicle; (17) uncinatc processes on first and second infrapharyngobranchials; (18) infrapharyngobranchials laterally supported; (19) differentiated dorsal gill arch musculature (i.e. presence of OD, TD, etc.); (20) four basibranchial copulae; (21) course of spinal nerves; (22) general similarities in pectoral girdle anatomy.

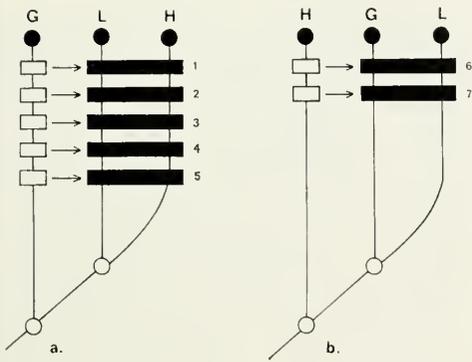


FIG. 18.—Alternate hypotheses of the phylogenetic position of the semionotiform genus *Lepidosteus* (L) to gars (G) and halecostomes (H). (a) Least rejected hypothesis, (b) alternate hypothesis with corroborating characters. Synapomorphies (black rectangles) connecting taxa are: (1) medial neural spines in caudal region; (2) a posterior myodome; (3) a supra-maxilla; (4) an interopercular; (5) a maxilla with internal articulatory head; (6) loss of opisthotic; (7) loss of epioccipital.

#### SYSTEMATIC ACCOUNTS

##### Division *Ginglymodi* Cope, 1872

Holostei Müller, 1845:119 (in part).

*Ginglymodi* Cope, 1872:328.

Rhomboganoidei Jordan and Evermann, 1896:108.

*Aetheospondylii* Goodrich, 1904:495; 1930:xvii (in part).

*Lepidosteoides* Goodrich, 1909:340.

*Orthoganoidei* Zittle and Koken, 1911:105.

*Lepisosteiformes* Hay, 1929:701 (in part).

*Lepisosteiformes* Berg, 1940:211.

*Semionotidea* Romer, 1966:353 (in part).

*Lepisosteida* Matsubara, 1955:170.

*Lepisosteii* Suttkus, 1963:61.

*Diagnosis.*—The ginglymods differ from all other actinopterygian fishes in the synapomorphous characters shown in Fig. 19. The more obvious characters for identification are: opisthocoelous vertebrae, plicidentine teeth, ethmoid elongation with snout bordered by toothed infraorbitals, premaxillary with nasal process carrying the supraorbital

canal, an atrophied maxillary, quadrate in front of orbit, cleithrum with medial wing, retractor muscles in upper gill arches not associated with the transverse dorsalis.

*Description and remarks.*—Body and head elongate. Body with interlocking ganoid scales covered with enameloid but lacking a dentine layer. Caudal fin semiheterocercal, without epaxial fin rays, with numerous haemal spines supporting fin rays, and numerous hypurals, epineurals, and ural centra; fulcral scales bordering the upper fin margin. Anal and dorsal fins far back on the body, caudal peduncle short. Anal and dorsal fins with fulcral scales on their anterior edges. Pelvic fins abdominal, internally supported by simple pectoral plates and without fulcral scales. Pectoral girdle consisting of dermal cleithrum, supracleithrum, and postcleithrum, without clavicle; endodermal mesocoracoid supporting radials and 11 to 14 fin rays. Vertebral column consisting of a series of opisthocoelous vertebrae with paired neural spines. Pleural ribs articulating with epipleural ribs that reach the outer body wall. Post-temporal an integral part of skull roof, without post-temporal process. Two to five small, rectangular supratemporals on each side of the midline. Parietals and dermopterotics equal in size and not conspicuously elongate. Frontals elongate. Premaxillary with a long process, carrying the supraorbital canal from the frontals to the nasals. Antorbitals and nasals crescent-shaped and small. Rostral U-shaped and carrying the infraorbital commissure. Snout bounded by three to ten toothed infraorbitals. Maxillary small and attached to the posterior infraorbital via tendon. Two or three lacrimals. A complete circumorbital series and a large mosaic of suborbitals. Opercular series consisting of an opercular, subopercular, and preopercular; no interopercular. Neurocranial ossifications including a medial basioccipital, paired exoccipitals, prootics, sphenotics, sphenoids, and a me-

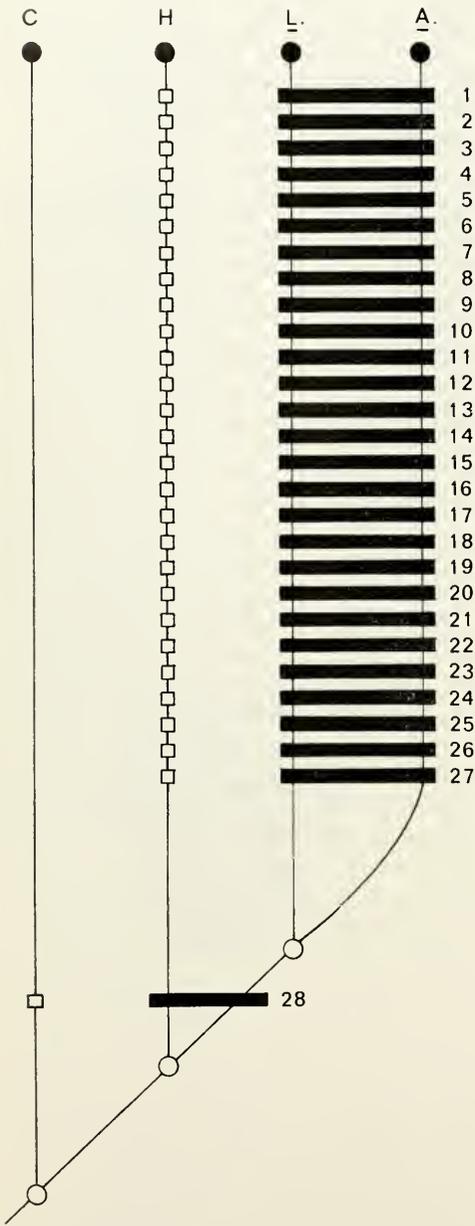


FIG. 19.—Phylogenetic analysis of the gar genera *Lepisosteus* (L) and *Atractosteus* (A) to the Halecostomi (H) and Chondrostei (C). Synapomorphies are black rectangles whereas plesiomorphies are white rectangles. Synapomorphous characters are: (1) no ethmoid ossifications; (2) elongate ethmoid region; (3) a series of toothed infraorbitals bordering the snout; (4) supraorbital canal on premaxillary process; (5) premaxillary process present, forming an external dermal component of the snout; (6) atrophied maxilla; (7) dermopter-

dial orbitosphenoid. Neurocranium lacking a dermal or endochondral intercalar, epiotics, or basisphenoid. Interorbital septum complete. Ethmoids cartilaginous. Parasphenoid long, flattened, grooved posteriorly for passage of the dorsal aorta, and extending from the posterior end of the basisphenoid to mid-snout. Basipterygoid process incorporating portions of both the parasphenoid and the prootics. Vomers overlying the parasphenoid anteriorly. Vomers elongate, paired, toothed, and lance-shaped. Quadrate in front of orbit, supported medially by the ectopterygoid and posteriorly by the quadratojugal. Hyomandibular and L-shaped symplectic not supporting the quadrate. Endopterygoids and metapterygoids articulating on the ectopterygoid and not contacting the quadrate or hyomandibular. Elongate ectopterygoid with teeth, overlain by dermopalatines anteriorly. Elongate, toothed dentary overlain by coronoids medially and with conspicuous meckelian groove on medial side extending  $1/3$  to  $1/2$  the length of the bone. Surangular and angular making up a coronoid process. Articulation of lower jaw via separate articular and retro-articular. Lateral posterior end of lower

otic-sphenotic articulation; (8) epioccipital lost; (9) postorbital commissure of supraorbital and infraorbital sensory canals on the dermopterotic; (10) ectopterygoid elongate; (11) autopalatine missing; (12) endopterygoid and metapterygoid not supporting the quadrate; (13) quadrate position in front of orbit; (14) symplectic "L" shaped and not contacting quadrate; (15) prearticular with lateral wing that restricts Meckel's cartilage; (16) mentomeckelian missing; (17) opisthotic and basisphenoid lost; (18) no anterior myodome; (19) a series of paired primary basihyal toothplates supported by a spatulate tongue; (20) a retro-articular-posterior ceratohyal ligament; (21) hypobranchials not penetrated by the ventral aorta; (22) medial toothplates reduced on visceral arches; (23) a retractor not associated with the transverse dorsalis; (24) a supra-cleithral process; (25) a medial wing on the cleithrum; (26) opisthocelous vertebrae; (27) plicidentine teeth; (28) synapomorphies uniting gars to other neopterygians: see figure 18a.

jaw overlain by the dermal angular. Hyoid arch without a basihyal and visceral arch without a fourth infrapharyngobranchial. A long series of paired primary basihyal tooth-plates. A single highly vascularized swimbladder. Conus arteriosus with seven tiers of eight valves, no bulbous arteriosus. Gut with spiral valve remnant. Females with oviduct directly connected to ovaries, males with staggered testes. Color pattern variable but primitively with dorsal flank and belly stripes.

*Lepisosteus sinensis* Bleeker (1873: 154) from China is a belonid, not a gar as reported by Wagner (1912:734). ?*Lepisosteus alessandrii* Ameghino (1898) from Argentina is listed by Pascual (1970) as an improbable member of the genus. *Litholepis adamantinus* Rafinesque (1818a:447) is a mythical fish drawn by J. J. Audubon (Suttkus, 1963: 69).

*Etymology*.—From the Greek *ginglymos*, a hinge joint, referring to the mode of articulation of the opisthocoelous vertebrae.

#### Family LEPISOSTEIDAE Cuvier, 1825

Lepisosteidae Cuvier, 1825:2, 307.  
Lepidostei Agassiz, 1832:140. Fitzinger, 1873: 52.  
Sauroides Agassiz, 1843:2.  
Lepidosteiin Müller, 1844:208. Carus, 1875: 590.

*Diagnosis and descriptive remarks*.—Those of the division Ginglymodi.

*Other remarks*.—The following nominal species are Lepisosteidae, genus and species indeterminate:

- †*Naisia apicalis* Münster, 1846:34 (Upper Eocene, Germany).
- †*Trichiuridea sagittidens* Winkler, 1876:31 (Middle Eocene, Belgium).
- †*Pneumatosteus nahunticus* Cope, 1869:242; 1875:31. Eastman, 1900a:68 (Miocene, North Carolina).
- †*Lepisosteus knieskerni* Fowler, 1911: 150 (?Cretaceous, New Jersey).

†*Atractosteus emmonsii* Hay, 1929: 709 (based on Emmons, 1858: 244; ?Miocene, North Carolina).

†*Paralepidosteus praecursor* Casier, 1961:42 (Early Cretaceous, Africa).

The following references refer to fossil gars for which no specific determination was attempted by the authors. Gidley, 1915:539 (Upper Cretaceous, Fort Union Fm., Montana); 1927:274 (Pleistocene, Florida). Gilmore, 1916:302 (Upper Cretaceous, New Mexico); 1920: 8, 68 (Upper Cretaceous, Kirtland Fm., Wyoming). Hay, 1903:120; 1927:274 (Pleistocene, Florida). Reeside, 1924:21, 23, 31, 38, 42 (Upper Cretaceous, Fruitland, McDermott, Ojo Alama, and Nacimiento Fms., New Mexico). Russel, 1935:118 (Cretaceous, Milk River Beds, Alberta). Bjork, 1967:229 (Eocene, Slim Buttes Fm., South Dakota).

#### *Lepisosteus* Lacépède

*Lepisosteus* Lacépède, 1803:331 (type species *L. gavialis* by subsequent designation, Jordan and Evermann, 1896:109).  
*Sarchirus* Rafinesque, 1818a:418 (type species *S. vittatus* by subsequent designation, Jordan, 1877:9).  
*Cylindrosteus* Rafinesque, 1820:72 (type species *C. platostomus* by subsequent designation, Jordan, 1877:11).  
*Lepidosteus* (Lacépède): Koenig, 1825:12; Agassiz, 1843:2.

*Diagnosis*.—Gars with an ectopterygoid-premaxillary articulation on the premaxillary process, without enlarged dermopalatine fangs, with projecting ridges above and below the articular socket of the supracleithrum. The frontal bone elongate anteriorly and posterolaterally, extending past the dermopterotic laterally to produce the characteristic shape of the frontal (Fig. 20). *Lepisosteus* also differs from *Atractosteus* in that *Lepisosteus* gars retain, primitively, small pear-shaped gill rakers (Fig. 21) and medial toothplates on the first infrapharyngobranchial (Fig. 22) and the first three hypobranchials and ceratobranchials.

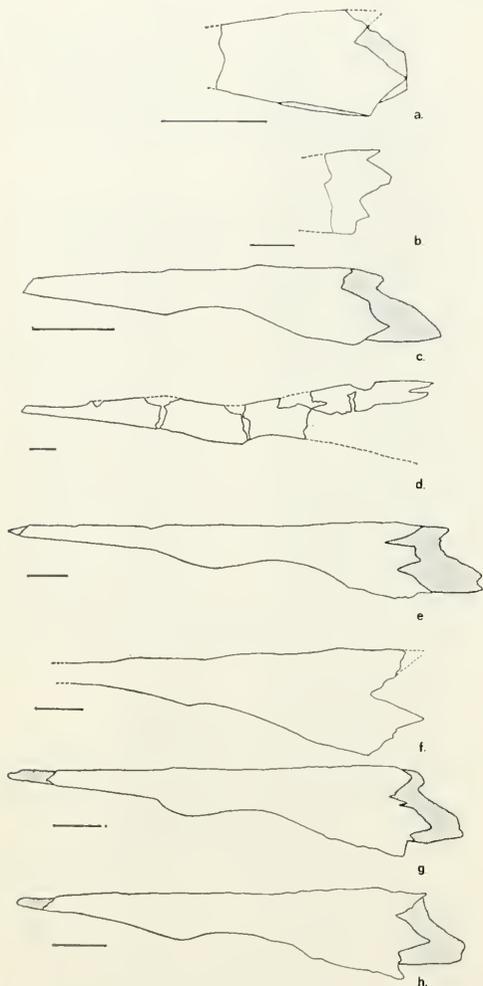


FIG. 20.—Frontal shape of eight *Lepisosteus*. (a.) *L. opertus* (MCZ P.13392); (b.) *L. cuneatus* (AMNH P.4622); (c.) *L. platostomus* (UMMZ 190846); (d.) *L. indicus* (BMNH P.12178); (e.) *L. osseus* (LACM 33917-4); (f.) *L. fimbriatus* (composite, BMNH P.1700 and P.13330); (g.) *L. oculus* (LACM 33915-1); (h.) *L. platyrhincus* (LACM 33912-2).

**Etymology.**—A compound masculine nominative derived from the Greek *lepis* (=scale) and Latin *osteus* (=bone).

The following nominal species and name combinations are *Lepisosteus* species indeterminate:

- †*Clastes cycliferus* Cope, 1873:634; 1877b:40; 1884:54. Woodward, 1895:415. Merrill, 1907:8 (Eocene, Wyoming).  
 †*Lepisosteus cycliferus* (Cope): Eastman, 1900a:68. Cockrell, 1908:163.

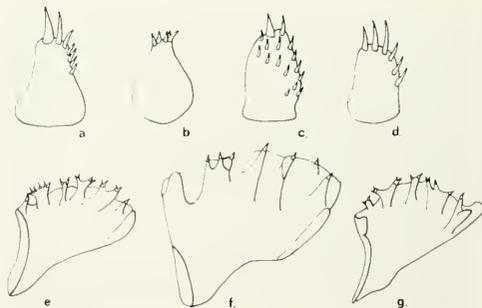


FIG. 21.—Gill rakers in seven Recent lepisosteids. (a.) *L. platostomus*; (b.) *L. osseus*; (c.) *L. oculus*; (d.) *L. platyrhincus*; (e.) *A. tristoechus*; (f.) *A. spatula*; (g.) *A. tropicus*.

†*Lepisosteus cycliferus* (Cope): Hay, 1902:337; 1929:377.

†*Lepisosteus longus* Lambe, 1908:13 (Oligocene, Saskatchewan, Canada).

The following references refer to Pleistocene and Pliocene records of *Lepisosteus*, sp. indet.: Hay (1927, Pleistocene of Florida); C. L. Smith (1954, Pleistocene of Oklahoma; 1958, Pleistocene of Oklahoma and Kansas; 1962, Lower Pliocene of Oklahoma); Uyeno and Miller (1962, Pleistocene of Texas; 1963, summary of North American records); Dalquest (1962, Pleistocene of Texas); Uyeno (1963, Pleistocene of Texas); Hibbard and Dalquest (1966, Pleistocene of Texas); Lundberg (1967, Pleistocene of Texas); Swift (1968, Pleistocene of Texas); and Wilson (1968, Pliocene of Kansas).

#### †*Lepisosteus opertus*, new species

Figures 20a, 23, 24a, 25a, 27a.

*Lepisosteus occidentalis*: Estes, 1964:43; 1969:11 (in part, bones of *A. occidentalis* mixed with bones of *L. opertus*).

**Diagnosis.**—*Lepisosteus opertus* differs from all other *Lepisosteus* in retaining the primitive enameloid pattern of the family on the dermopterotics and parietals (Figs. 25a, 27a).

**Types.**—The holotype (MCZ P.13392) is an incomplete frontal (Figs. 20a, 23a). Paratypes include two fragmentary fron-

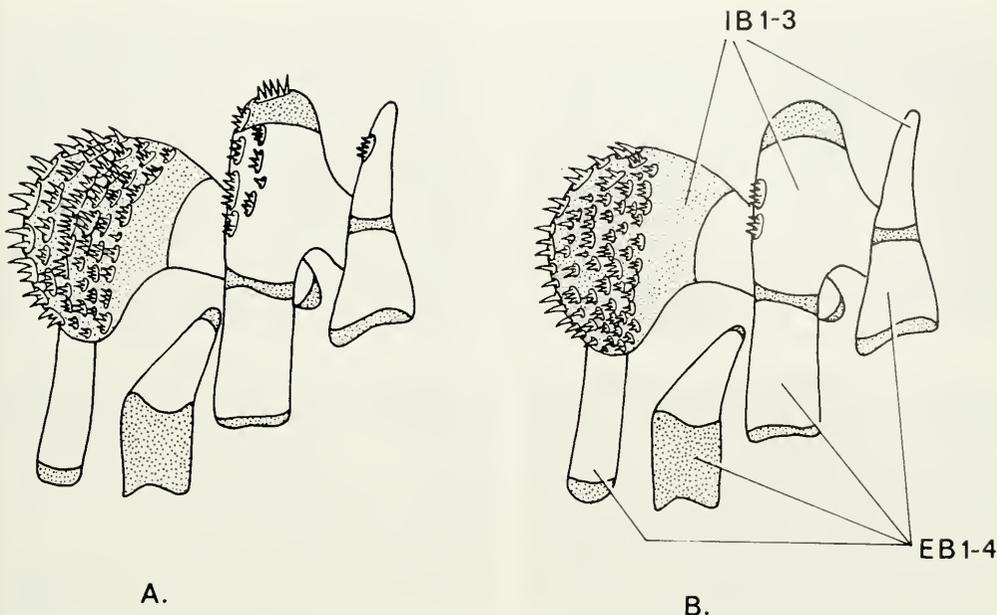


FIG. 22.—Ventral views of the upper gill arch elements of (A) *Lepisosteus oculatus* and (B) *Atractosteus tropicus*. Semidiagrammatic; cartilage stippled. EB 1-4, epibranchials 1-4; IB 1-3, infrapharyngobranchials 1-3.

tals (MCZ P.13396), two dermopterotics (MCZ P.13397, Fig. 23b), one preopercular (MCZ P.13393, Fig. 23c), 17 infraorbitals (MCZ P.13394-95), three parietals (MCZ P.9374, Fig. 27a).

*Type locality*.—Bug Creek Anthills, section map locality SW 1/4-9-T22N-R43E (or approximately 25 mi. SSE of Ft. Peck), McCone County, Montana.

*Formation and age*.—Hell Creek Formation, Upper Cretaceous, probably in other formations such as the Lance, and Belly River series.

*Description and comparisons*.—*Lepisosteus opertus* is a small Cretaceous gar known only from fragmentary remains. No counts or measurements were obtainable.

All premaxillaries from the Hell Creek formation have a double row of premaxillary teeth, but I cannot assign the smaller preserved premaxillaries to either *A. occidentalis* or *L. opertus*. I assume that *L. opertus* had two complete rows of premaxillary teeth like *L. platostomus*. The dermopalatines are

unknown. Infraorbitals are narrow and elongate, with rounded enameloid tubercles. Circumorbitals have enameloid, but the condition of the dorsal circumorbital and relationship of the dermosphenotic to the orbital margin is unknown. The number of supratemporals per side is unknown. Supracleithrum has a long bony process on the ventral side of the articular facet (Fig. 24a).

Frontal shape is like that of other *Lepisosteus* (Fig. 20a), and it has rows of rounded enameloid tubercles along the bony ridges. Shape and enameloid pattern of the dermopterotic and parietal can be compared to other *Lepisosteus* shown in Figs. 25a and 27a.

*Lepisosteus opertus* differs from *Atractosteus* gars in the shape of the posterior end of the frontal bone (Fig. 20a). *Lepisosteus opertus* differs from *Atractosteus occidentalis* in that *L. opertus* has enameloid on the frontals, infraorbitals, circumorbitals, and preopercular, whereas *A. occidentalis* lacks enameloid or has only occasional, minute, rounded, enameloid tubercles on the

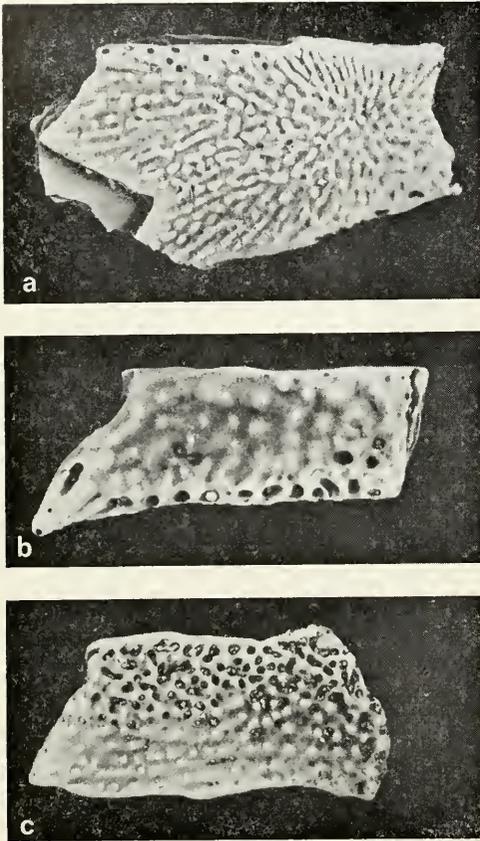


FIG. 23.—Various bones of *Lepisosteus opertus*. (a.) Frontal (MCZ P.13392, 21mm, holotype); (b.) infraorbital (MCZ P.13395, 13 mm, paratype); (c.) preopercular (MCZ P.13393, 23-mm, paratype).

preopercular. In addition, *L. opertus* has sheets of enameloid on the parietals and dermosphenotics and elongate infraorbitals and a *Lepisosteus* supraclithrum, whereas *A. occidentalis* has rounded enameloid tubercles on the dermosphenotic, square infraorbitals, and a supraclithrum more like that of *A. spatula*, *A. tristoechus*, and *A. atrox*.

*Etymology*.—From the Latin, *opertus* (=hidden), referring to the observation that it has remained undescribed among the material assigned to another species, *A. occidentalis*.

### †*Lepisosteus cuneatus* (Cope)

Figs. 20b, 25b, 27b, 29b, 31, 32

*Clastes cuneatus* Cope, 1878:9; 1880:303; 1884:55.

*Lepisosteus cuneatus*: Eastman, 1900a:68; 1900b:57. Hay, 1902:377; 1929:708. Hussakof, 1908:78. Cockerell, 1909:796. Hussakof and Bryant, 1919:195. Stromer, 1925:360.

*Diagnosis*.—Differs from all other *Lepisosteus* in that the width of the opercular and subopercular is greater than the distance from the margin of the opercular apparatus and the suborbitals anterior to the medio-posterior orbital margin, whereas in all other *Lepisosteus* the width of the opercular and subopercular is less than this distance.

*Type*.—AMNH P.2517. A complete fish with crushed skull displaying a large opercular typical of the species.

*Type locality*.—Manti Beds, Central Utah. No exact locality given.

*Formation and Age*.—Green River Formation, Lower Eocene.

*Descriptive comments*.—*Lepisosteus cuneatus* is a small, short-snouted gar from the Eocene of North America. Details of the posterior half of the skull of AMNH P.4622 in dorsal and lateral view are shown in Fig. 31. Meristic data are shown in Table 2.

Presence or absence of second premaxillary tooth row not determined. Dermopalatine without dermopalatine fangs. Five to six infraorbitals. Number of circumorbitals not determined, but dermosphenotic included in the orbital margin and there are three circumorbitals forming the posterior orbital margin. Three lacrimals. Few suborbitals (AMNH P.4623, Fig. 32). Opercular and subopercular large compared to postorbital head length. Two supratemporals on each side of the midline. Supracleithrum only partly observable, condition of articular facet not observable.

Frontal shape, as far as determinable, characteristic of the genus (Fig. 25b). Shape and enameloid pattern of dermo-

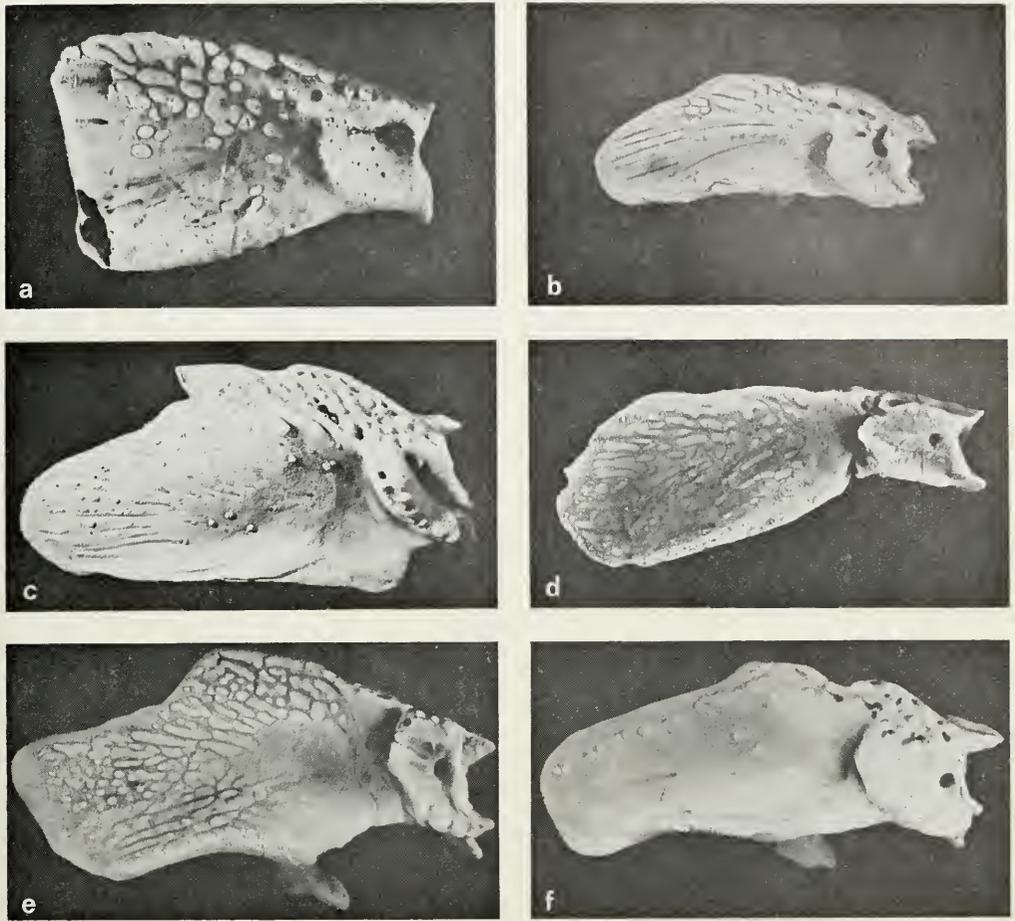


FIG. 24.—Supracleithra of six *Lepisosteus* species. (a.) *L. opertus* (AMNH P.9323); (b.) *L. platostomus* (AMNH 7147, 27mm); (c.) *L. osseus* (LACM 33916-4, 16mm); (d.) *L. fimbriatus* (BMNH P.1300, 24mm); (e.) *L. oculatus* (LACM 33914-3, 20mm); (f.) *L. platyrhincus* (LACM 33912-4, 17mm).

pterotic, parietal, and opercular shown in Figs. 25b, 23b, and 29b, respectively. All skull bones with large amounts of enameloid in the form of broad, elongate continuous tubercles or large, rounded tubercles.

Differs from *L. opertus* in having a reduced number of convoluted and inter-connected enameloid ridges on the dermopterotics and parietals, and in other details of enameloid pattern (Figs. 25b, 27b). Differs from *L. fimbriatus* and all Recent *Lepisosteus* in having wide interconnecting enameloid ridges on the parietals and dermopterotics, and

dorsal half of the opercular, and in having large, rounded enameloid tubercles on other parts of these bones, whereas in *fimbriatus* and Recent *Lepisosteus* the enameloid is thinner, and usually occurs as disconnected tubercles (reduced in many species to series of small, rounded tubercles). Differs from *L. indicus* in that *cuneatus* has enameloid and a short snout, whereas *indicus* lacks enameloid and has a long snout (Fig. 20).

*Etymology.*—From the Latin *cuneatus* (=wedge-shaped), referring to the skull of the type.

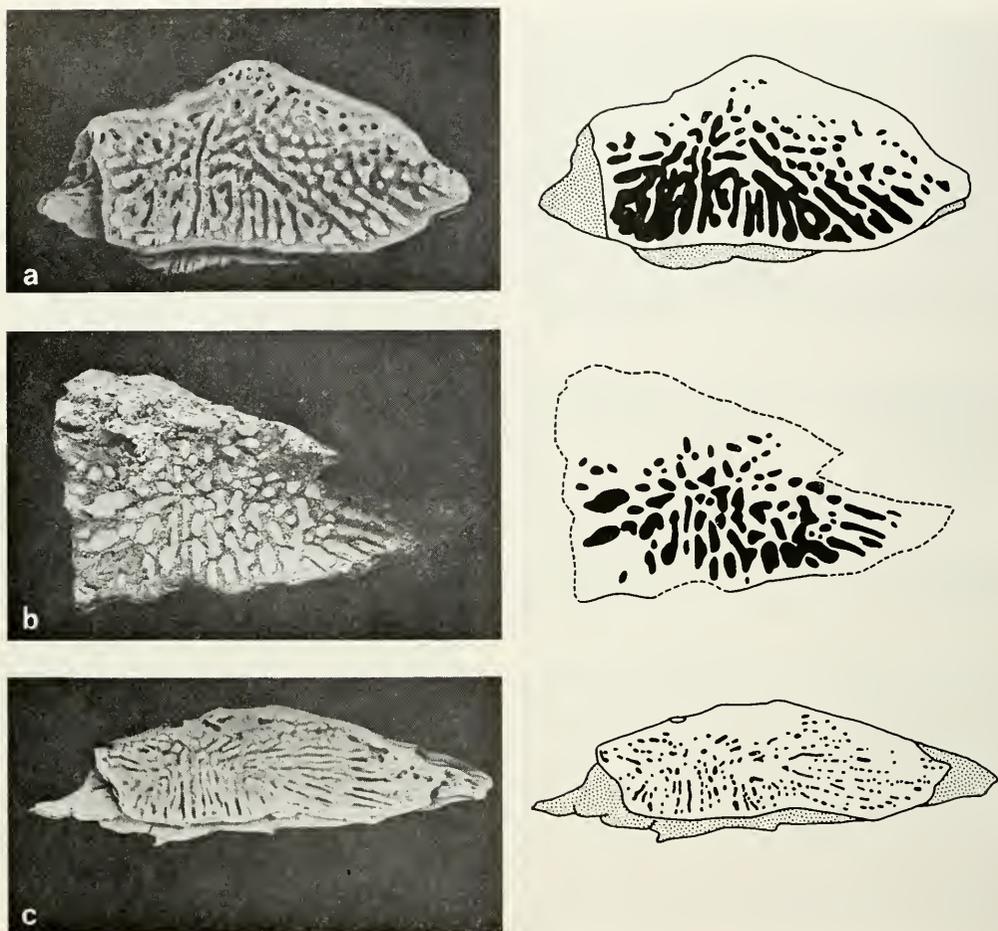


FIG. 25.—Dermopterotics of three *Lepisosteus*. (a.) *L. opertus* (MCZ P.13397, paratype, 27mm); (b.) *L. cuneatus* (AMNH P.4622, 23mm); (c.) *L. platostomus* (UMMZ 190846R, 25mm).

### *Lepisosteus platostomus* Rafinesque

#### SHORTNOSE GAR

Figs. 20c, 21a, 24b, 25c, 27c, 29b, 33, 34a

*Lepisosteus platostomus* Rafinesque, 1820:72.  
Jordan and Evermann, 1896:110. Suttkus,  
1963:71.

*Lepisosteus albus* Rafinesque, 1820:73.

*Lepisosteus platystomus* Günther, 1870:329.  
Jordan and Gilbert, 1883:91. Jordan, 1885:  
13.

*Cylindrosteus scabiceps* Fowler, 1910:607. Jor-  
dan, Evermann and Clark, 1930:37.

*Cylindrosteus platostomus*: Jordan, Evermann,  
and Clark, 1930:37.

**Diagnosis.**—Differs from other *Lepi-*  
*sosteus* except *L. opertus* in having two  
complete rows of premaxillary teeth (up

to 8 in *L. platostomus*, 2-4 in *L. osseus*,  
1-2 in *L. oculus*, *L. platyrhinchus*, and  
*L. fimbriatus*). Differs from *L. opertus*  
in having thin enameloid ridges usually  
disconnected into oblong tubercles,  
whereas *L. opertus* has wide, intercon-  
nected tubercles.

**Type.**—No type material was col-  
lected by Rafinesque.

**Descriptions and comparisons.**—A  
small gar without flank stripes or belly  
pigmentation in adults. A typical skull  
is shown in Fig. 33. Meristic counts are  
shown in Table 2 and various morpho-  
metric measurements expressed as ra-  
tios or dorsal head length are shown in  
Tables 3 and 4.

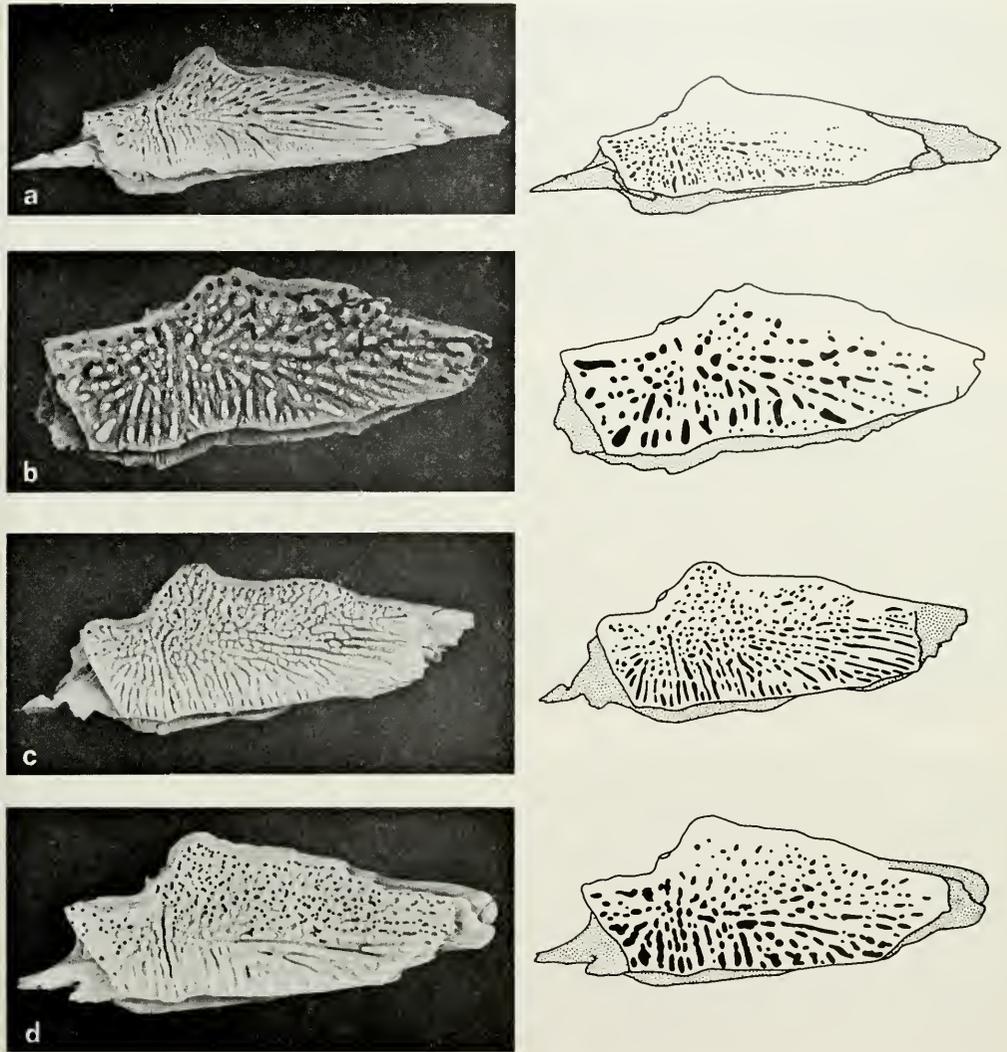


FIG. 26.—Dermopterotics of four *Lepisosteus*. (a.) *L. osseus* (LACM 33917-4, 30mm); (b.) *L. fimbriatus* (BMNH P.1700, 27mm); (c.) *L. oculatus* (LACM 33915-1, 32mm); (d.) *L. platyrhincus* (LACM 33912, 30mm).

Head and dorsum darker than flank and belly. Flank stripe variable, usually indistinct or same intensity as dorsum. Flank usually with a series of vertical pigment bars between some scale rows. Usually two distinct pigment blotches on caudal peduncle immediately in front of caudal fin. Flank stripe more distinct on cheek and may be broken into two stripes on the opercular as an individual variation, continuing through eye and ending on coronoid process of lower jaw. Juveniles with faint preopercular and retroarticular stripes, these absent or diffuse in adults. Mid-dorsal stripe absent or faint. Gular region with some pigment bordering medial margin of lower jaw. Belly

without belly stripes or pigment blotches. Pectoral and pelvic fins without transverse pigment bars. Anal and dorsal fins with two or three transverse rows of pigment blotches. Caudal fin with variable pigment blotches on fin rays and fin membranes.

Premaxillary process with ridges for articulation of ectopterygoid and with two complete rows of premaxillary teeth. Dermopalatine with two tooth rows, the inner row of adults somewhat enlarged but not as large as infraorbital fangs. Seven to nine infraorbitals. Eight to ten circumorbitals, dorsal circumorbital not enlarged, demnosphenotic included in the orbital margin, three circumorbitals including the der-

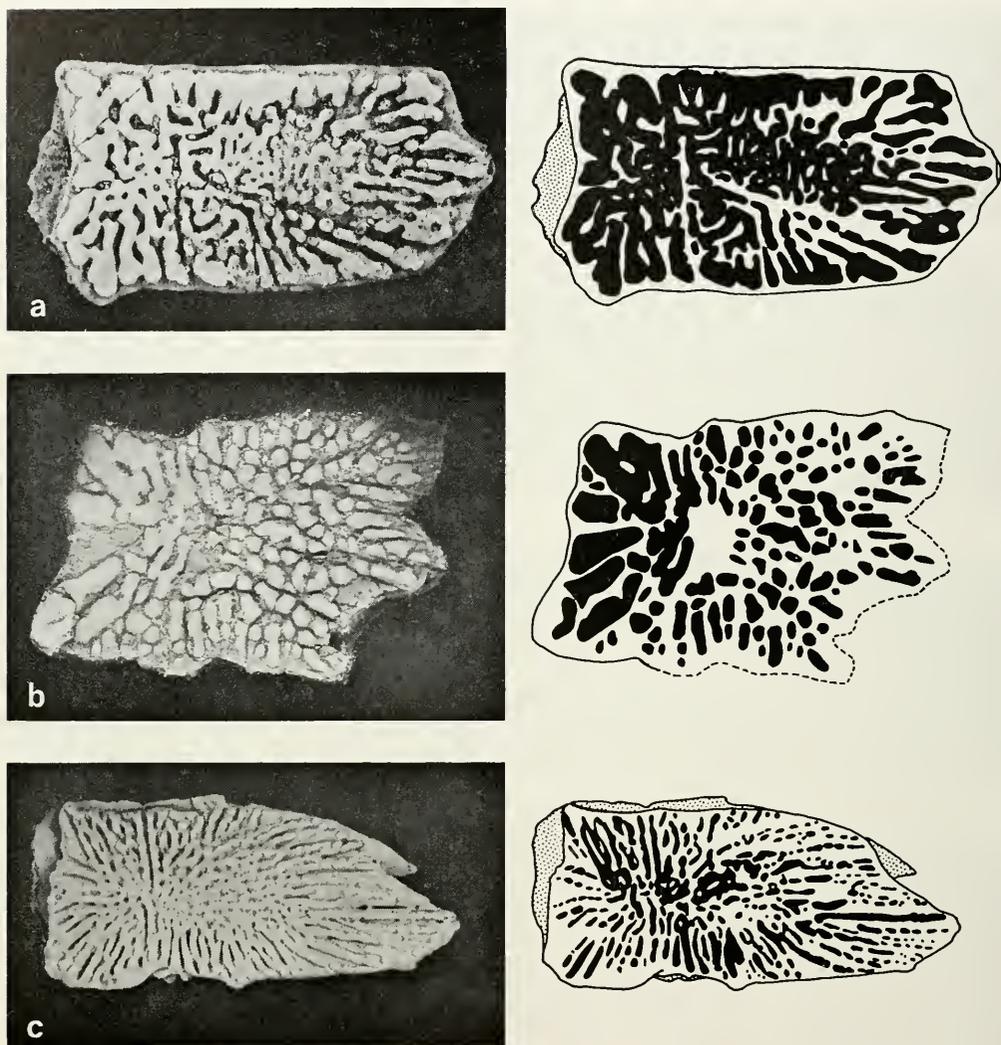


FIG. 27.—Parietals of three *Lepisosteus*. (a.) *L. opertus* (MCZ P.9374, 24mm); (b.) *L. cuneatus* (AMNH P.4622, 21mm); (c.) *L. platostomus* (UMMZ 190846, 21mm). Enameloid pattern shown in black on outline drawings.

mosphenotic forming posterior orbital margin. Three lacrimals. Suborbitals not numerous, the ventro-posterior marginal suborbitals distinctly larger than those of the internal mosaic. Two or four supratemporals on each side of midline. Supracleithrum with projections above and below articular facet, its shape shown in Fig. 24b.

Enameloid on all dermal roofing bones of skull. These bones with low-lying bony ridges capped by more or less continuous elongate enameloid tubercles. Shape and enameloid pattern of dermopterotic, parietal, and opercular shown in Figs. 25c, 27c, and 29c, respectively.

First basihyal toothplate paired. Gill rakers small, pearshaped (Fig. 21a), and not numer-

ous (Table 2). A single row of medial toothplates on the first arch. A single complete row of medial toothplates on second and third lower arch elements and two complete rows on the fourth arch (Fig. 34a), a single row of medial toothplates on first infrapharyngobranchial, two rows on the second infrapharyngobranchial.

Differs from *L. osseus* and *L. indicus* in that *L. platostomus* has a shorter snout. Differs from *L. oculatus* and *L. platyrhincus* in number of lateral line scales (59-65 in *platostomus*, 53-59 in *oculatus* and *platyrhincus*) and head color pattern (blotched in *oculatus* and *platyrhincus* plain in *platostomus*).

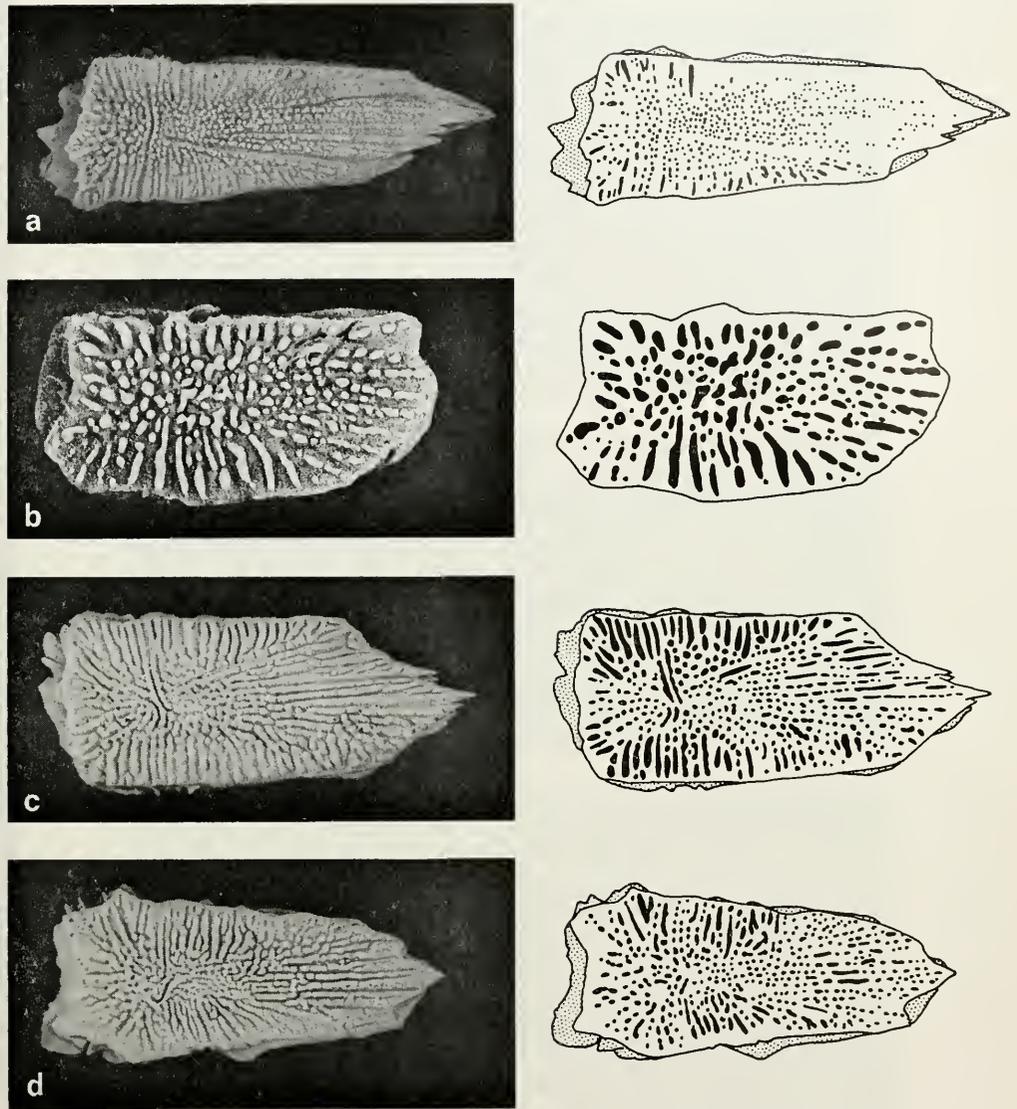


FIG. 28.—Parietals of four *Lepisosteus*. (a.) *L. osseus* (LACM 33917-4, 38mm); (b.) *L. fimbriatus* (BMNH P.33525, 19mm); (c.) *L. oculatus* (LACM 33915-1, 36mm); (d.) *L. platyrhincus* (LACM 33912-2, 33mm). Enameloid patterns shown in black on outline drawings.

*Etymology*.—From the Greek *plator* (=broad or flat) and *stomus* (= mouth).

*Range*.—Northeastern Texas north to Montana, east to southern Ohio and south to Mississippi (Schultz, 1965).

*Other comments*.—Schultz (1965) and G. R. Smith (1964) report *L. platostomus* from the Pleistocene of Kansas. A report from Florida by Hay (1917) is considered by Uyeno and Miller (1963) to be *L. platyrhincus*.

### *Lepisosteus osseus* (Linnaeus)

#### LONGNOSE GAR

Figs. 10, 15, 20d, 21b, 24c, 26a, 28a, 29c, 34b, 35

*Esox osseus* Linnaeus, 1758:313.

*Esox viridis* Gmelin, 1789:1389 (In: Linnaeus, 1789; not *Lepisosteus viridis* Günther, which is *A. spatula*).

*Lepisosteus gavalis* Lacépède, 1803:333.

*Sarchirus vittatus* Rafinesque, 1818a:419.

?*Lepisosteus stenorrhynchus* Rafinesque, 1818b:

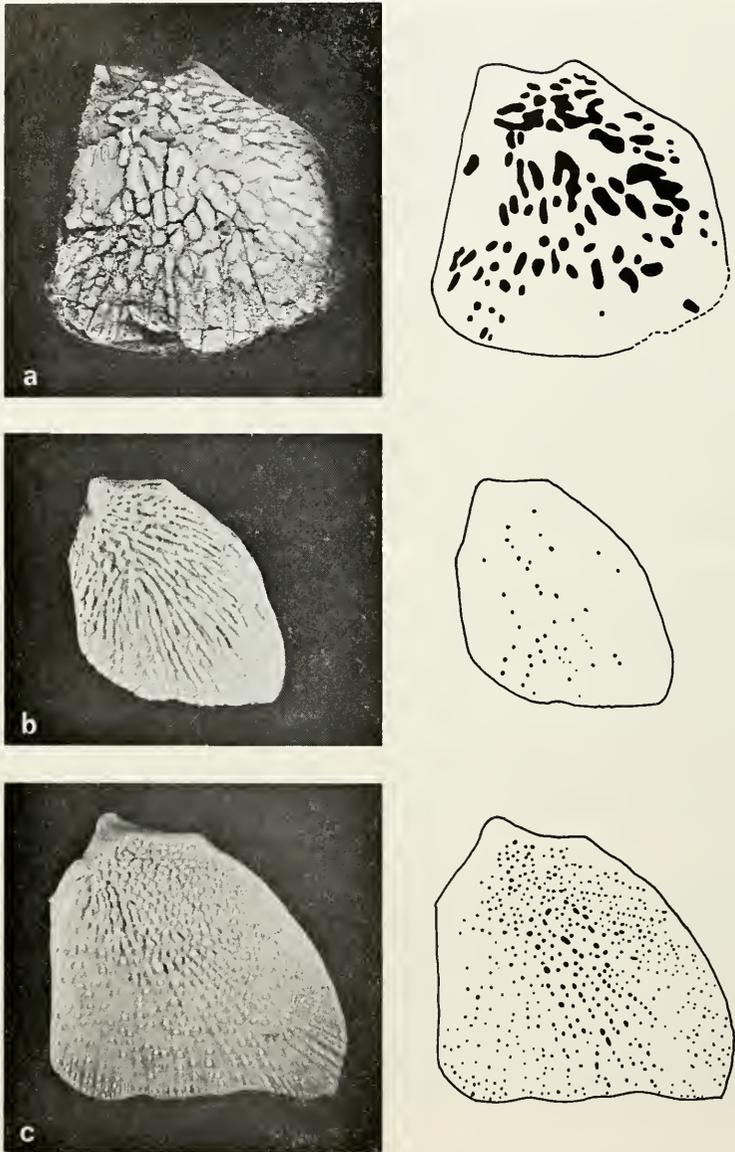


FIG. 29.—Operculars of three *Lepidosteus*. (a.) *L. cunctatus* (AMNH P.4622, 20mm); (b.) *L. platostomus* (UMMZ 190846, 11mm); (c.) *L. osseus* (LACM 33917-4, 21mm). Enameloid patterns shown in black on outline drawings.

447 (listed by Suttkus, 1963, as a doubtful synonym).  
*Lepidosteus oxyurus* Rafinesque, 1820:73.  
*Lepidosteus longirostris* Rafinesque, 1820:74.  
 ?*Sarchinus argenteus* Rafinesque, 1820:86 (listed by Suttkus 1963, as a doubtful synonym).  
*Lepidosteus osseus*: Agassiz, 1843:2. Günther, 1870:330.  
*Lepidosteus semiradiatus* Agassiz, 1843:2.  
*Lepidosteus gracilis* Agassiz, 1843:2.  
*Lepidosteus huronensis* Richardson, 1836:237.

*Lepidosteus rostratus* Cuvier, 1836:238 (In: Richardson, 1836).  
*Lepidosteus bison* De Kay, 1842:271.  
*Lepidosteus lineatus* Thompson, 1842:145.  
*Macrogathus loricatus* Gronow, 1854:148.  
*Lepidosteus leptorhynchus* Girard, 1858:351.  
*Lepidosteus otarius* Cope, 1865:86.  
*Lepidosteus erassus* Cope, 1865:86.  
*Lepidosteus treculi* Duméril, 1870:327.  
*Lepidosteus mulberti* Duméril, 1870:228.  
*Lepidosteus harlani* Duméril, 1870:329.

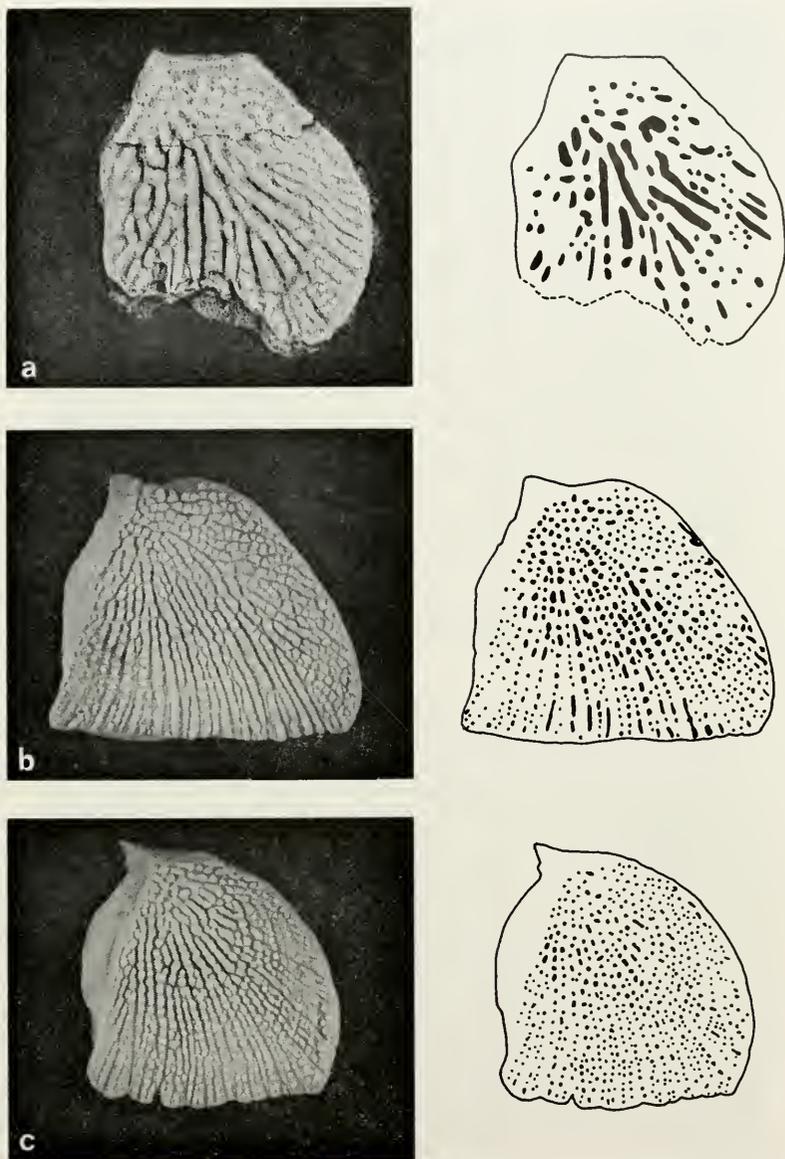


FIG. 30.—Operculars of three *Lepidosteus*. (a.) *L. fimbriatus* (BMNH P.1529, 14mm); (b.) *L. oculatus* (LACM 33915-1, 24mm); (c.) *L. platyrhincus* (LACM 33912-2, 20mm). Enameloid patterns shown in black on outline drawings.

*Lepidosteus smithi* Duméril, 1870:330.  
*Lepidosteus ayresii* Duméril, 1870:331.  
*Lepidosteus copei* Duméril, 1870:332.  
*Lepidosteus lesueurii* Duméril, 1870:335.  
*Lepidosteus elisabeth* Duméril, 1870:336.  
*Lepidosteus lamarii* Duméril, 1870:337.  
*Lepidosteus clintonii* Duméril, 1870:338.  
*Lepidosteus troostii* Duméril, 1870:339.  
*Lepidosteus piquotiamus* Duméril, 1870:340.  
*Lepidosteus horatii* Duméril, 1870:341.  
*Lepidosteus thompsoni* Duméril, 1870:342.

*Lepidosteus louisianensis* Duméril, 1870:343.  
*Lepidosteus osseus*: Suttkus, 1963:79.

*Diagnosis*.—*Lepidosteus osseus* differs from all other Recent species of the genus in having an extremely attenuated snout (snout length 79% to 83% of dorsal head length in *osseus*, less than 75% in other species).

*Type*.—A dried specimen with bro-

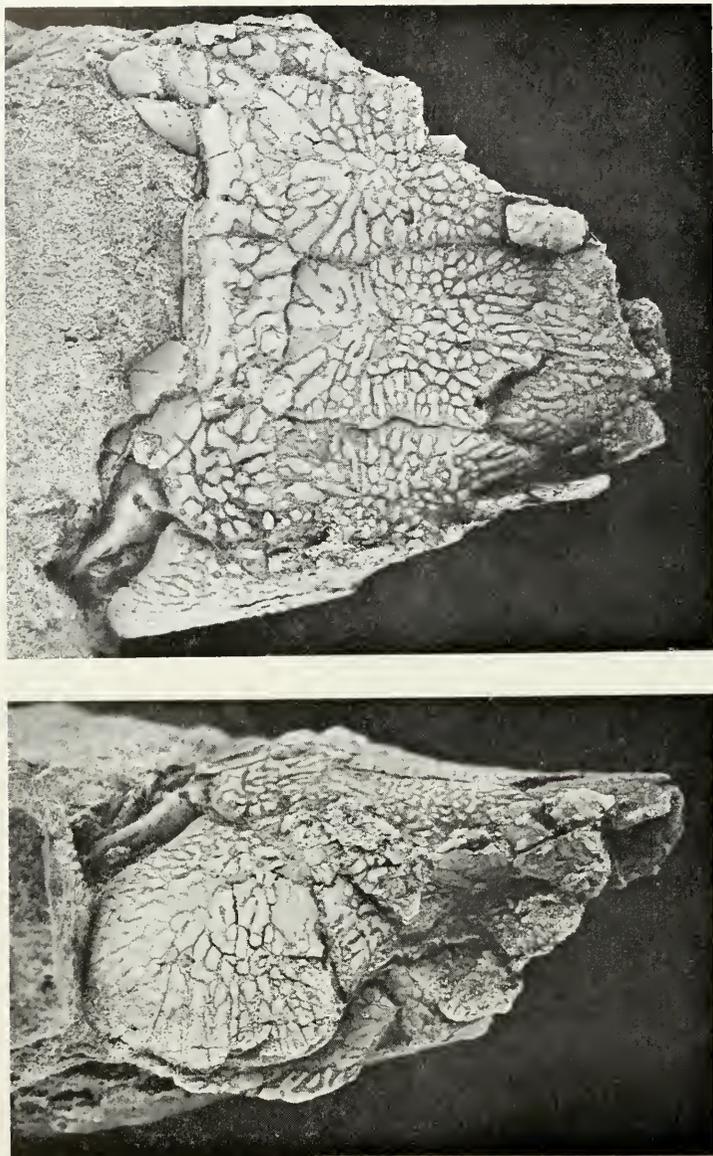


FIG. 31.—Dorsal (upper) and lateral (lower) views of the posterior skull of *L. cuneatus* (AMNH P.4622, 38mm from back of skull to anterior end in dorsal view).

ken snout on deposit in the Linnean Collection of the Linnean Society of London.

*Description and comparisons.*—*Lepisosteus osseus* is a medium sized (to 1500 mm, Suttkus, 1963) gar with a narrow attenuated snout. The skull of a typical individual is shown in Fig. 35. Various count data shown in Table 2. Morphometrics expressed as ratios of

dorsal head length shown in Tables 3 and 4.

Color pattern of adults varying with environmental conditions (Suttkus, 1963:77). Juveniles with continuous mid-dorsal stripe missing in adults, where dorsum darkened by general melanophore development. Flank stripe of juveniles continuous from base of caudal fin through eye onto lower jaw. Flank stripe of juveniles serrate on upper margin. Adult flank stripe either missing or reduced to a series of

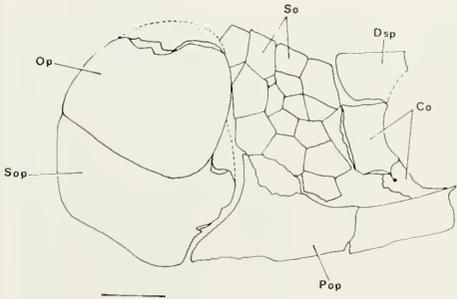


FIG. 32.—Medial view of the post-orbital region of *Lepisosteus cuneatus* (AMNH P.4623, 60mm). Co, circumorbital; Dsp, dermosphenotic; Op, opercular; Pop, preopercular; So, suborbital, Sop, subopercular.

pigment blotches. Preopercular stripe incomplete. Head with or without small random pigment blotches. Posterior half of lower jaw with scattered melanophores. Gular region with pigment lining lower jaw, such pigment extending from symphysis to branchiostegals. Isthmus with or without scattered pigment of variable intensity. One belly stripe per side in juveniles, extending from pectoral base to anal fin, where stripes fuse on the ventrum of caudal peduncle. Belly between stripes usually unpigmented; belly stripes usually missing in adults.

Pectoral fin base pigmented in juveniles, usually unpigmented in adults. Pectoral fins with 2-5 transverse rows of pigment blotches. Pelvic fins with two rows of transverse pigment blotches. Anal and dorsal fins usually with three transverse rows of pigment blotches. Caudal fin with numerous pigment blotches, pattern individually variable. Urostyle of juveniles unpigmented.

Premaxillary with outer tooth row of two to four teeth. Dermopalatine of adults without fangs, both rows of teeth small in adults. Nine to ten circumorbitals, dorsal circumorbital not enlarged, dermosphenotic included in orbital margin, three circumorbitals comprising posterior orbital border including the dermosphenotics. Eight to ten long, thin infraorbitals. Suborbitals not numerous, marginal suborbitals larger than internal mosaic. Three lacrimals. Two to three supratemporals on each side of midline. Supracleithrum with bony projections above and below articular facet, its shape distinctive compared with other *Lepisosteus* (Fig. 24c).

Frontal shape shown in Fig. 20d, frontal attenuated, frontal enameloid reduced. Shape and enameloid pattern of the dermopterotic, parietal, and opercular shown in Figs. 26a, 28a, and 29c respectively.

Differs from *L. oculatus*, *L. platyhincus*, and *L. fimbriatus* in that *L. osseus* has two to

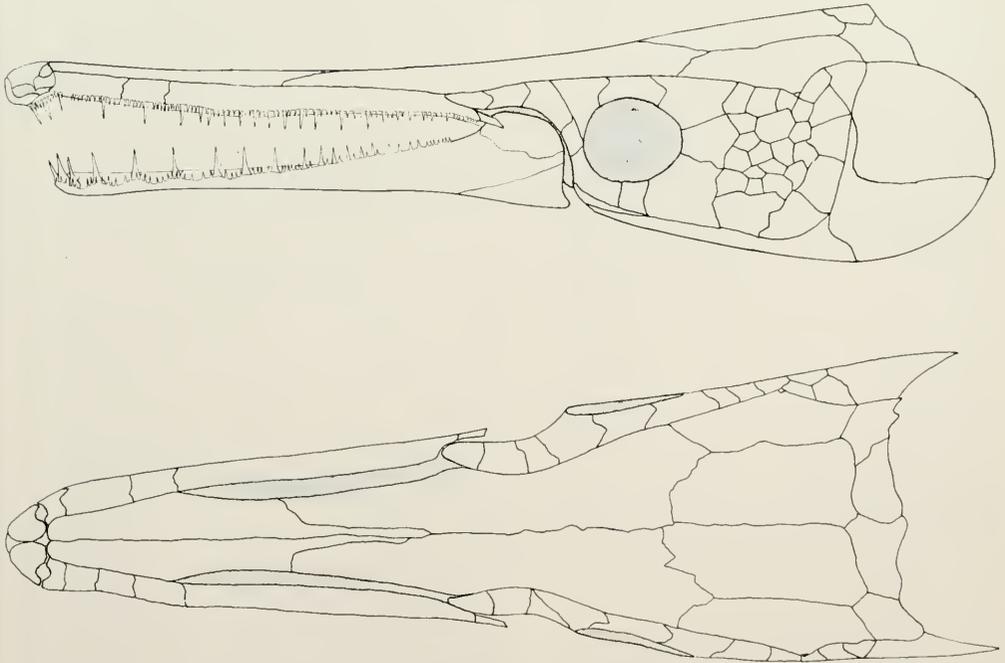


FIG. 33.—Lateral (upper) and dorsal (lower) views of the skull of *Lepisosteus platostomus* (UMMZ 190846, DHL-82mm).

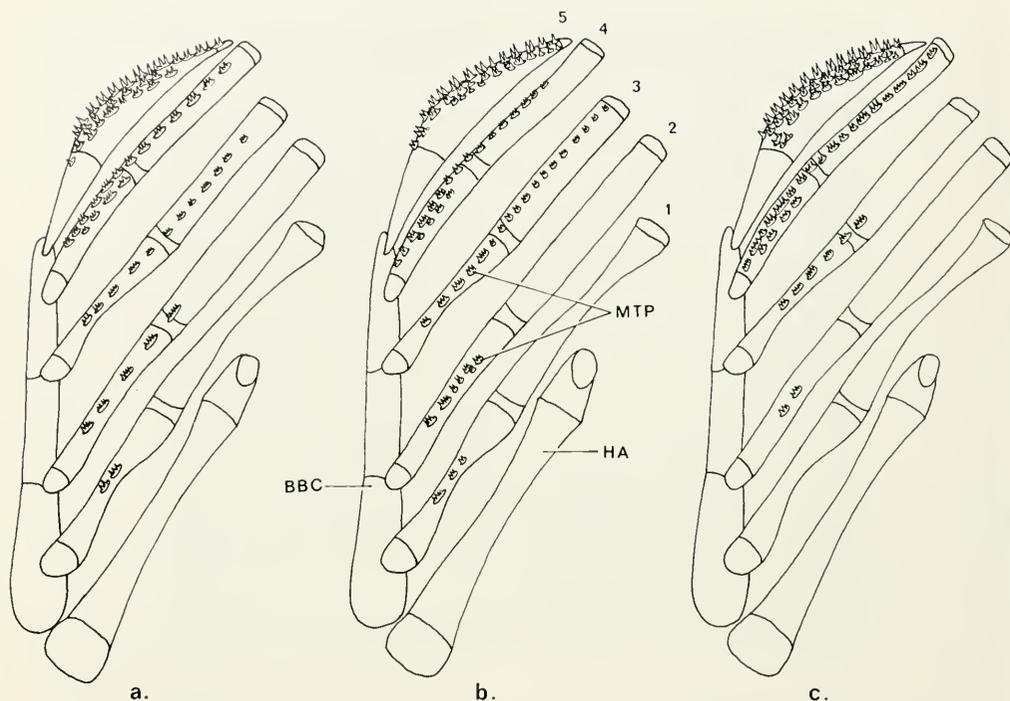


FIG. 34.—Semidiagrammatic dorsal view of the left lower gill arches of three *Lepisosteus*. (a.) *L. platostomus*; (b.) *L. osseus*; (c.) *L. oculatus* (*L. platyrhincus* is similar to c.). Gill rakers omitted; cartilage stippled. BBC, basibranchial copula; HA, hyoid arch; MTP, median tooth plate; 1-5, gill arches 1-5.

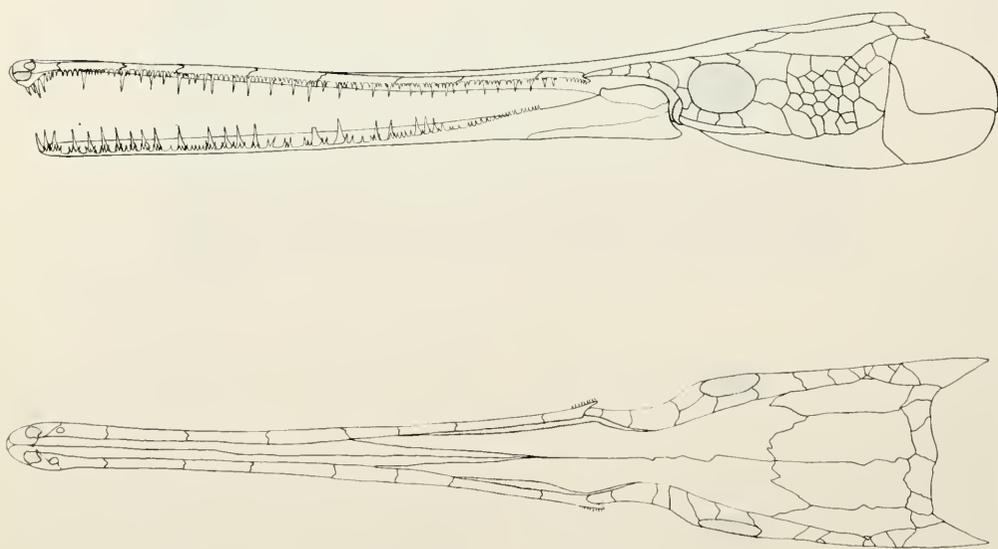


FIG. 35.—Lateral (upper) and dorsal (lower) views of the skull of *Lepisosteus osseus* (AMNH uncat., DHL-224mm).

four teeth in outer row of premaxilla, others with a single medial tooth in outer row (rarely two in *platyrhincus*). Also differs from *L. oculatus* and *L. platyrhincus* in that *osseus* lacks large pigment blotches on head (and other details of juvenile and adult color patterns) and has paired first basihyal toothplates, whereas *oculatus* and *platyrhincus* have large pigment blotches on head and fused first basihyal toothplates. Differs from *L. platostomus* and *L. opertus* in that *L. osseus* has incomplete outer row of premaxillary teeth, whereas the above species have complete outer row of teeth. Also differs from *L. platostomus* in juvenile and adult color pattern and from *L. opertus* in that the latter has wide interconnected enameloid ridges on parietals and dermopterotics, whereas *osseus* has thin continuous tubercles or series of round or oblong tubercles on these bones that are not interconnected. Differs from *L. indicus* in that *osseus* has enameloid on the dermal skull bones, whereas *indicus* lacks enameloid.

*Etymology*.—From the Latin *osseus* (=bone).

*Range*.—Quebec to Florida along the Atlantic coast; westward to the Great Lakes region and south to northern Mexico and western Texas.

*Other comments*.—*Lepisosteus osseus* has been reported from the Pleistocene of North Carolina (Hay, 1923) and Kansas (Schultz, 1965; Neff, 1975). Archeological reports include Keenlyside et al. (1974).

### †*Lepisosteus indicus* (Woodward)

Figs. 20e, 36

*Belonostomus* (?) *indicus* Woodward, 1890:23; 1895:439.

*Lepidosteus indicus* Woodward, 1908:2.

*Diagnosis*.—Differs from all other *Lepisosteus* in having dermal bones without ridges or enameloid.

*Type*.—BMNH P.12178, a crushed skull, also vertebrae, and scales (BMNH P.12185, P.12186) figured by Woodward, 1908.

*Type Locality*.—Lameta Beds, Don-gargoan, Madhya Pradesh, Central Province, India.

*Formation and Age*.—Lameta Formation, Upper Cretaceous.

*Description and comments*.—The skull (BMNH P.12178) is crushed with the dorsal side showing (Fig. 36). There is no counterpart. The vertebrae are figured by Woodward (1908) and are either on deposit in India or lost.

*Lepisosteus indicus* is a long-snouted gar with no dermal skull ornamentation. Both frontals are partly preserved, elongate, and most similar to *L. osseus* (Fig. 20e). Right frontal 160 mm in length, left frontal is too fragmentary to measure. Both premaxillaries are partly preserved. Ascending process of premaxillary a significant part of snout roofing bones, typically

TABLE 2.—Ranges of various meristic counts for seven species of gars.<sup>1</sup>

| Character                       | Species               |                  |                    |                        |                    |                   |                       |
|---------------------------------|-----------------------|------------------|--------------------|------------------------|--------------------|-------------------|-----------------------|
|                                 | <i>L. platostomus</i> | <i>L. osseus</i> | <i>L. oculatus</i> | <i>L. platyrhincus</i> | <i>A. tropicus</i> | <i>A. spatula</i> | <i>A. tristoechus</i> |
| No. predorsal scales .....      | 50-55                 | 47-55            | 45-54              | 47-51                  | 42-48              | 49-54             | 49-51                 |
| No. lateral line scales .....   | 59-65                 | 57-63            | 53-59              | 54-59                  | 41-56              | 58-62             | 56-63                 |
| No. transverse scale rows ..... | 21-24                 | 19-24            | 18-24              | 21-25                  | 20-24              | 23-32             | 21-24                 |
| No. dorsal fin rays .....       | 8-9                   | 6-9              | 6-9                | 7-8                    | 7-8                | 7-10              | 7-8                   |
| No. anal fin rays .....         | 8-9                   | 8-10             | 7-9                | 7-8                    | 7-8                | 7-10              | 7-8                   |
| No. caudal fin rays .....       | 11-12                 | 11-14            | 12-13              | 12-13                  | 11-12              | 12-14             | 11-12                 |
| No. pectoral fin rays .....     | 11-12                 | 10-13            | 9-13               | 9-11                   | 11-12              | 11-15             | 11-12                 |
| No. gill rakers ..              | 27-33                 | 14-31            | 15-24              | 19-33                  | 59-62              | 59-66             | 67-81                 |

<sup>1</sup> Some data from Suttkus (1963).

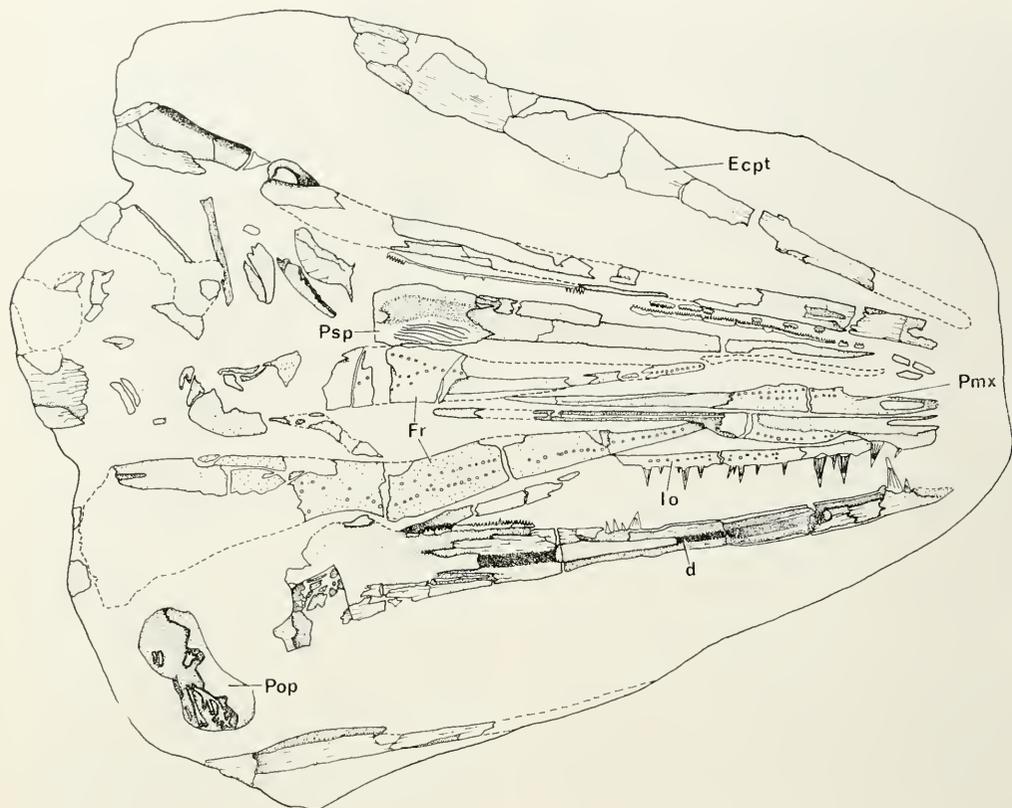


FIG. 36.—Type skull of *Lepisosteus indicus*. d, dentary; Ecpt, ectopterygoid; Fr, frontal; Io, infraorbital; Pmx, premaxilla; Pop, preopercular; Psp, parasphenoid.

gar-like, carrying part of supraorbital canal. Left lower jaw is exposed with its inner surface showing; 181 mm from tip of retroarticular to broken anterior end. Posterior articular series is fragmentary. Articular-retroarticular articulating surface is concave, similar in shape to that in other gars. Inner surface of dentary broken, exposing meckelian groove. Both large and small plicidentine teeth are preserved. Part of right infraorbital chain is preserved. Woodward (1908:4) incorrectly identified this series of three infraorbitals as "palato-ptyergoid arcade." Additional preparation revealed articulations between infraorbitals and infraorbital sensory canal pores. Infraorbitals lack bony ridges or enameloid. One circumorbital was identified. Hyomandibular fragmentary, similar to that of other gars. Parasphenoid (partly preserved) lies between the frontals. Left ectopterygoid preserved, plus fragments of vomers and dermopalatines. No indication of dermopalatine dentition. One bone, which fits into position of supraorbital on frontal concavity, does not carry infraorbital canal (like that of *Lepisosteus*, but not *Atractosteus*). One canal-bearing bone, tentatively identified as circum-

orbital, is located left of the partly preserved hyomandibular.

*Etymology*.—The trivial name *indicus* refers to the country of occurrence.

#### †*Lepisosteus fimbriatus* Wood

Figs. 20f, 24d, 26b, 28b, 30a, 37, 38a

*Lepidotus fimbriatus* Wood, 1846:6, 122.

*Lepisosteus suessionensis* Gervais, 1852:4; 1859:517; 1874a:846; 1874b:459. Dollo, 1893:193. Leriche, 1900:188; 1902:44; 1907:243; 1923:183, 186; 1932:369. Priem, 1901:489; 1908:81, 86, 90, 98. White, 1931:80. Casier, 1943:2.

*Lepisosteus maximilliani* Vasseur, 1876:295.

*Lepisosteus* sp.: Rutot, 1884:XV.

*Lepisosteus fimbriatus*: Woodward, 1895:442.

*Diagnosis*.—Differs from all *Lepisosteus* except *L. oculatus* and *L. platyrhincus* in that *L. fimbriatus* and the two other species have a single medial tooth

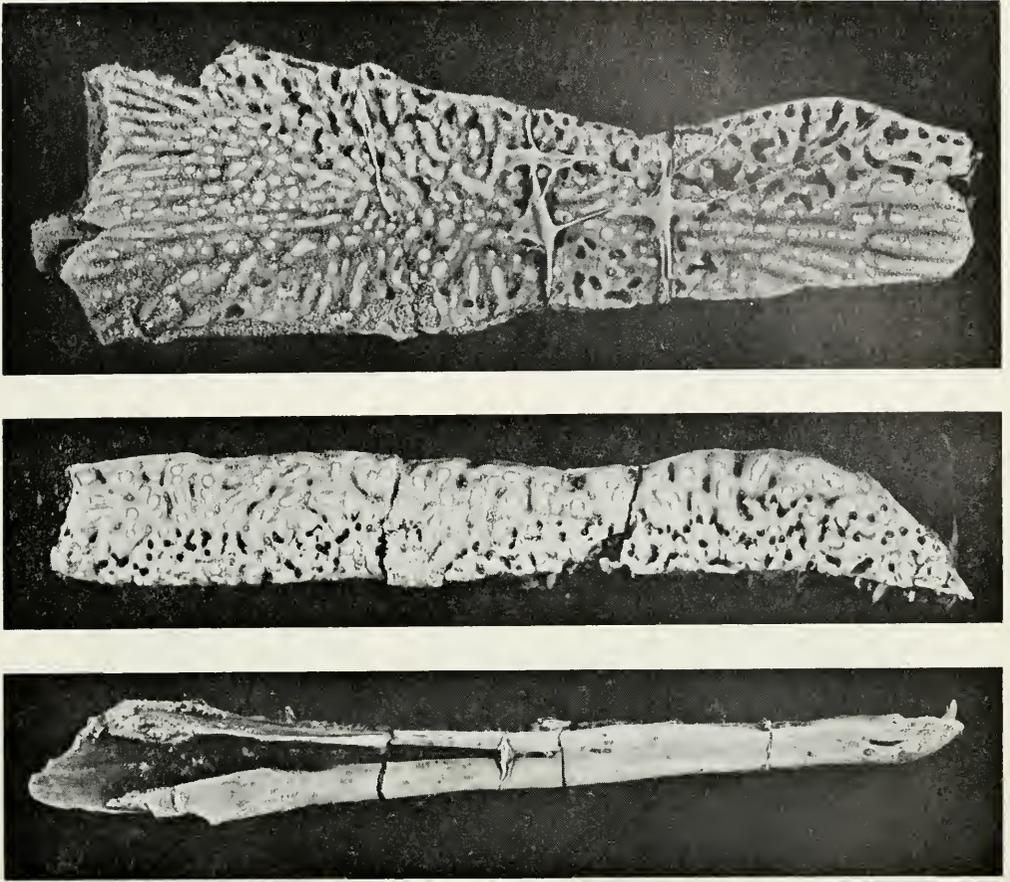


FIG. 37.—Various bones of *Lepisosteus fimbriatus*. (a.) dentary (BMNH P.1300, 49mm); (b.) partial infraorbital series (BMNH P.33522, 39mm); (c.) frontal (BMNH P.1300, 36mm).

on the outer tooth row of the premaxillary (Fig. 37a). Differs from *L. oculatus* and *L. platyrhincus* in details of the shape and enameloid pattern of the dermopterotic, parietals, and supraclathrum. Differs from *L. indicus* in frontal bone shape (Fig. 20), and in that *L. fimbriatus* has enameloid, whereas *L. indicus* lacks enameloid. Differs from *A. strausi* in that *A. strausi* has sheets of enameloid on the dermopterotics, parietals, frontals, and supratemporals, whereas *L. fimbriatus* has elongate to oval enameloid tubercles on these bones.

*Types*.—BMNH P.25252 (partial dentary) and P.25254 (opercular).

*Formation and age*.—Known from most freshwater Eocene and lower Oli-

gocene deposits of Belgium, France, and England.

*Description and comments*.—All specimens of *L. fimbriatus* studied were small. Various skull elements not shown elsewhere are found in Fig. 37. No meristics or morphometrics were obtainable.

Premaxillary with single medial tooth on outer tooth row (Fig. 37a). Dermopalatines of BMNH P.1300 with small fangs comparable to fangs on small *L. platostomus*. Six infraorbitals (BMNH P.33522). Number of circumorbitals indeterminate, dermosphenotic included in orbital margin. Number of lacrimals indeterminate. Preserved suborbitals could not be counted. Two to four supratemporals on each side of midline. Supraclathrum with small bony projections above and below articular facet, its shape compared to other *Lepisosteus* shown in Fig. 24.

Frontal shape like other relatively short-nosed *Lepisosteus* (Fig. 20). Shape and enameloid pattern of dermopterotic, parietal, and opercular compared to other *Lepisosteus* shown in Figs. 26b, 28b, 30a. Enameloid pattern and shape of other bones shown in Fig. 37. Vertebral centrum ovoid, ventral ridges not wide, transverse process not wide. Scales smooth.

*Etymology*.—From the Latin *fimbriatus* (=bordered with hairs or fibrous), referring to the enameloid pattern of the opercular.

*Other comments*.—Some vertebrae from the Blackheath Beds are subtriangular, have wide transverse processes and widely spaced ventral ridges similar to *A. strausi*. No dermal skull bones assignable to *A. strausi* have been collected in these beds, but collection of additional specimens may show its presence in the Upper Eocene and Lower Oligocene of England. Casier's (1943) figures may include a lower jaw of *Atractosteus*. Specimens referred to by Gervais (1859, 1874a, 1874b) as *L. suessionensis* include bones identical to British *L. fimbriatus*, as well as bones identified here as *Amia* sp. indet.

## *Lepisosteus oculatus* Winchell

### SPOTTED GAR

Figs. 2, 8, 20g, 21c, 22a, 24e, 26c, 28c, 30b, 34c, 38b

?*Lepisosteus latirostris* Girard, 1858:352 (placed in synonymy with *C. castelnaudi*=*L. oculatus* by Jordan, Evermann, and Clark, 1930:37).

*Lepisosteus oculatus* Winchell, 1864:183. Suttkus, 1963:71.

*Cylindrosteus productus* Cope, 1865:86.

*Cylindrosteus agassiz* Duméril, 1870:347. Jordan, Evermann, and Clark, 1930:37.

*Cylindrosteus bartonii* Duméril, 1870:347.

?*Cylindrosteus zadocki* Duméril, 1870:353.

*Lepisosteus platostomus* Jordan and Evermann, 1896:110 (in part; *L. oculatus* listed as synonym of *L. platostomus*).

*Cylindrosteus castelnaudii*: Jordan, Evermann, and Clark, 1930:37 (in part).

*Lepisosteus productus*: Hubbs and Lagler, 1943:76. Eddy, 1957:40.

*Diagnosis*.—Differs from all extant *Lepisosteus* except *L. platyrhincus* in having large pigment spots on the head,

having a single medial tooth in the outer premaxillary tooth row, and no medial toothplates on the first visceral arch. Differs from *L. platyrhincus* in that adults have bony ossicles on the ventral isthmus surface under the gill membrane, whereas *L. platyrhincus* lacks these ossicles (Suttkus, 1963).

*Type*.—UMMZ 55062, a whole dry preserved specimen.

*Description and comparisons*.—This species is a gar of medium size and proportion, reaching a reported length of 819 mm total length (Suttkus, 1963). The skull of a typical specimen is shown in Fig. 2. Meristic counts are shown in Table 2. Various skull measurements expressed as ratios of dorsal skull length are shown in Tables 3 and 4. Females have proportionately longer snouts than males (Hubbs and Lagler, 1943; Suttkus, 1963).

*Lepisosteus oculatus* shows much variation in color pattern intensity, especially belly pigmentation. Generally dark above, lighter on flank. Flank stripe continuous in young, usually broken into series of blotches in adults, running from caudal peduncle anteriorly through eye, onto lower jaw, there fusing with the preopercular stripe. Preopercular stripe usually continuous, occasionally broken. Retroarticular spot present; may not contact flank stripe in front of orbit. Head with numerous large pigment blotches on dorsal surface. Edges of the infraorbitals with distinct pigment dashes. Gular region mottled to solid over its entire area, extending onto isthmus. One belly stripe per side, usually interconnected by reticulate pigment blotches between stripes. Some adults with uniformly dark belly pigment obliterating belly stripes, others without belly pigmentation. Belly stripes unite at anal fin and continue posteriorly as a single stripe. Pectoral and pelvic fins of adults with as many as five transverse pigment bars, juveniles with as few as two. Lower half of pectoral finbase dark. Dorsal, anal, and caudal fins with varying numbers of pigment blotches.

Premaxilla with ridges on process for articulation of the ectopterygoid and with a single medial tooth in the outer tooth row. Dermo-palatine with two tooth rows, inner row in adults not enlarged as fangs. Six to eight infraorbitals. Eight to nine circumorbitals with the dorsal circumorbital not enlarged and the dermosphenotic incorporated into orbital margin. Three circumorbitals forming posterior margin

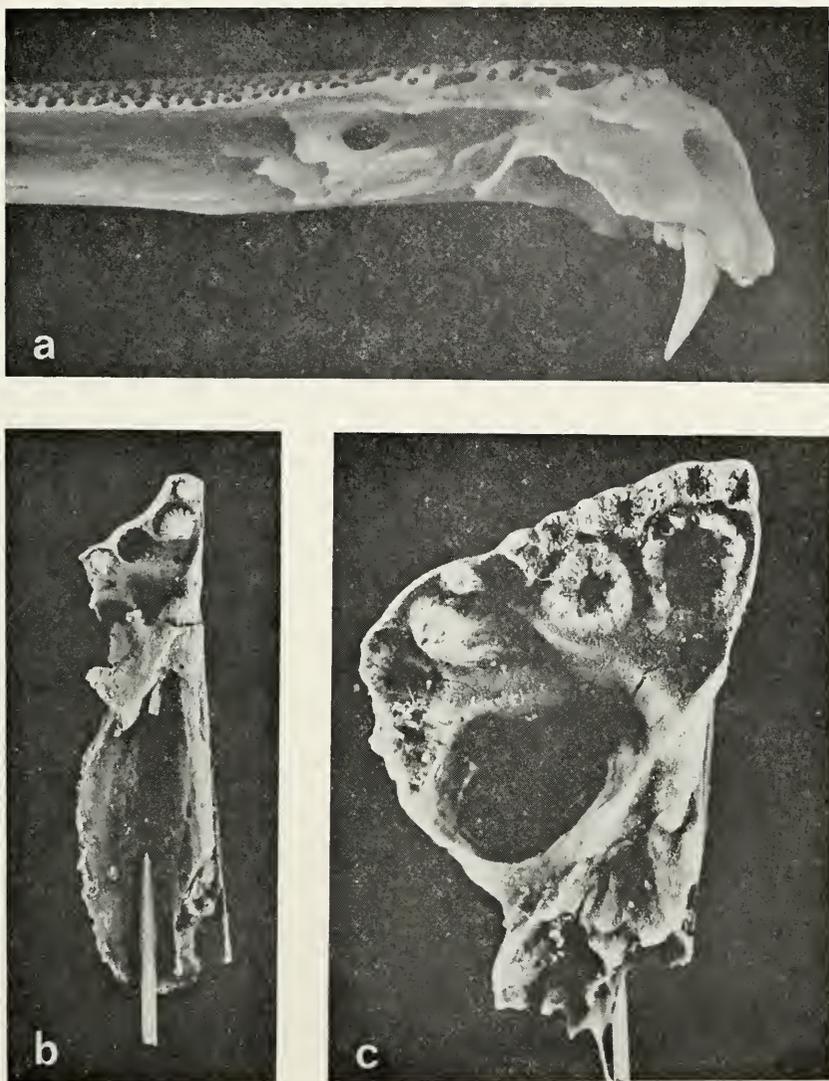


FIG. 38.—Premaxillas of three gar species. (a.) *Lepisosteus oculatus* (LACM 33915-1, tol. length 60mm); (b.) *L. fimbriatus* (BMNH P.1300, 17mm); (c.) *Atractosteus occidentalis* (AMNH P.9323, 19mm).

of the orbit. Three lacrimals. Suborbitals not numerous. The ventral-posterior marginal suborbitals larger than internal mosaic.

Two to four supratemporals on each side of midline. Supracleithrum with projecting ridges above and below articular facet, its shape most similar to that of *L. platyrhincus* (Fig. 24e).

Dermal skull bones with elongate enameloid tubercles and rounded tubercles. Frontal shape shown in Fig. 20g. Shape and enameloid patterns of the dermopterotic, parietals, and opercular shown in Figs. 26c, 28c, and 30b, respectively.

First basihyal toothplate fused. Gill rakers

small and pear-shaped (Fig. 21c) numbering 15 to 24 on the first arch outside row (Table 2). Medial toothplate pattern shown in Fig. 34c. Medial toothplates missing on first arch, reduced on second arch to a single row on the hypobranchial, reduced to a single row on the third and fourth arches. Medial toothplates missing on the first infrapharyngobranchial.

*Lepisosteus oculatus* differs from *L. platostomus* in number of lateral line scales (53-59 in *L. oculatus*, 59-65 in *L. platostomus*, Suttkus, 1963) and from *L.*

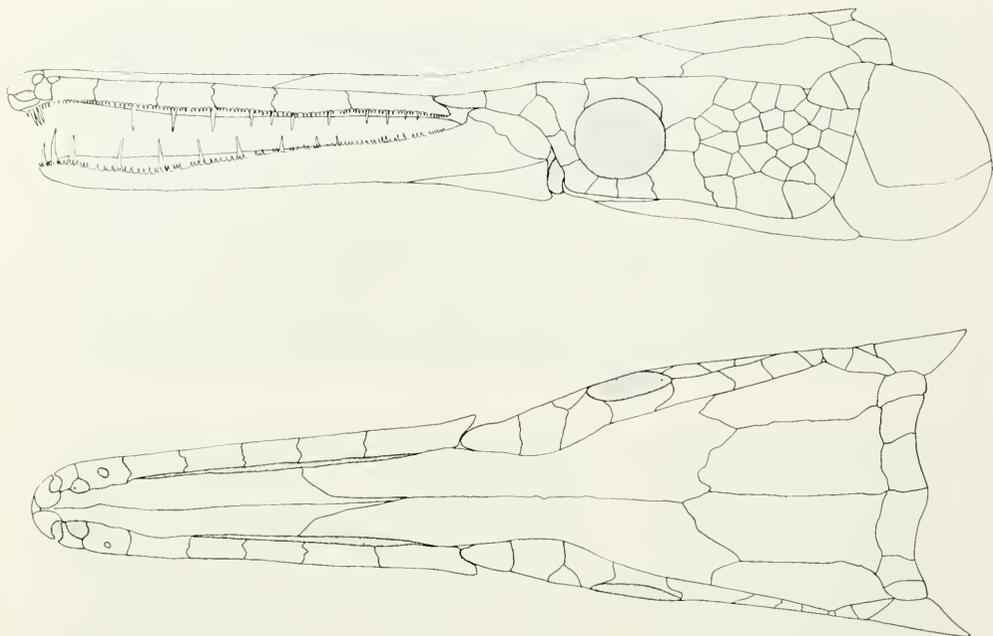


FIG. 39.—Lateral (upper) and dorsal (lower) views of the skull of *L. platyrhincus* (UMMZ 159805-1, DHL-126 mm).

osseus in snout length. *Lepisosteus oculatus* differs from *L. fimbriatus* in that the medial wing of the cleithrum of *L. oculatus* is large, whereas in *L. fimbriatus* it is small. *L. oculatus* differs from *L. indicus* in frontal bone proportions and in that *L. oculatus* has enameloid on dermal bones of the skull, whereas *L. indicus* lacks enameloid.

*Etymology*.—From the Latin *oculus* (=eye) and *atus* (=provided with).

*Range*.—From the Great Lakes south to the Gulf of Mexico, eastward along the Gulf Coast to Western Florida and westward to Central Texas (Suttkus, 1963).

### *Lepisosteus platyrhincus* De Kay

#### FLORIDA SPOTTED GAR

Figs. 20h, 21d, 24f, 26d, 28d, 30c, 39

*Lepisosteus platyrhincus* De Kay, 1870:355.  
Suttkus, 1963:83.

*Cylindrosteus castelnaudi* Duméril, 1870:355.  
Jordan, Evermann, and Clark, 1930:37.

*Lepisosteus platostomus*: Jordan and Evermann, 1896:111 (in part).

*Cylindrosteus megalops* Fowler, 1910:609. Jordan, Evermann, and Clark, 1930:37 (mentioned as doubtful).

*Diagnosis*.—Differs from all *Lepisosteus*, where the character is known, except *L. oculatus* and *L. fimbriatus* in having one (occasionally two) medial teeth on the outer premaxillary tooth row as opposed to having uniformly two or more teeth on the outer premaxillary tooth row.

*Type*.—Not examined. Supposedly on deposit at the Lyceum, Alexandria, Virginia.

*Description and comparisons*.—*Lepisosteus platyrhincus* is a medium sized gar (to 1,330 mm total length; Hammett and Hammett, 1936) and usually is darkly pigmented. A skull is shown in Fig. 39. Meristics taken in this study and reported by Suttkus (1963) are shown in Table 2. Morphometrics taken from a small series and expressed as ratios of dorsal head length are shown in Tables 3 and 4.

Color patterns of adults showing polymorphic variation in color intensity (from "im-

maculate" to very dark individuals from same localities, Suttkus, 1963). Dorsal stripe continuous in juveniles, adults with uniform dark or mottled dorsum. Flank stripe in young from base of caudal fin through the eye, and to tip of the lower jaw. Flank stripe of adults usually broken into series of darker and lighter blotches. Juveniles with stripe between dorsal and flank stripes from nape to one-half the distance between pectoral and pelvic fins. Belly with one or two belly stripes per side, fusing at anal fin to form one stripe on caudal peduncle. Most individuals with belly mottled between belly stripes. Head with large pigment blotches on dorsum. Preopercular and retroarticular stripes fused, and usually fused with flank stripe just anterior to eye. Gular region usually solidly pigmented, isthmus mottled. Pectoral fin base pigmented. Three to five transverse rows of pigment blotches on pectoral and pelvic fins. Dorsal and anal fins with three or four transverse rows of pigment blotches. Caudal fin with many randomly placed pigment blotches. Other color notes given by Suttkus (1963).

Premaxilla with single medial tooth on outer tooth row (occasional individuals have two teeth on one side, one tooth on other). Dermopalatine of adults without enlarged fangs. Eight to ten circumorbitals, dorsal circumorbital not enlarged, dermosphenotic included in orbital margin. Three circumorbitals comprising posterior orbital margin, including dermosphenotic. Six to seven infraorbitals. Three lacrimals. Suborbitals not numerous, marginal suborbitals larger than internal mosaic. Supracleithrum with bony projections above and below articular facet; shape of supracleithrum shown in Fig. 24f. Shape and enameloid pattern of dermopterotic, parietal, and opercular shown in Figs. 26d, 28d, and 30c, respectively.

*Lepisosteus platyrhincus* differs from *L. platostomus* in that *platyrhincus* has large pigment blotches on the head (none in *platostomus*) and fewer lateral line scales (54-59 in *platyrhincus*, usually 59-65 in *platostomus*). *L. platyrhincus* differs from *L. osseus* in that *osseus* either has small pigment blotches on the head or lacks them and has a narrow snout, whereas *platyrhincus* has large pigment blotches on the head and a wider snout (least width of snout 12.9-25.7 times in snout length in *osseus*, 4.8-8.2 in *platyrhincus*; Suttkus, 1963). Differs from *L. indicus* in shape of the frontal bone (relatively shorter in *platyrhincus*, Fig. 20). Differs from *L. cuneatus* in that *cuneatus* has wide enam-

eloid tubercles on the dermopterotics and parietals whereas *L. platyrhincus* has series of rounded tubercles or relatively thin elongate tubercles on these bones (Figs. 26, 28, and 30 respectively).

*Etymology*.—From the Greek *platys* (=flat) and *rhynchos* (=snout).

*Range*.—From the southern tip of Florida northward to the lowlands of Georgia (Suttkus, 1963).

*Other comments*.—Fowler's (1917) report of *L. platostomus* from the Pleistocene of Florida is considered by Uyeno and Miller (1963) to be *L. platyrhincus*. Suttkus (1963) gives saltwater and ecological references.

### *Atractosteus* Rafinesque

*Atractosteus* Rafinesque, 1820:75 (type species *A. ferox* by subsequent designation, Jordan, 1877:11).

*Clastes* Cope, 1873:633 (type species herein designated *C. atrox* Cope, 1873:633).

*Clasticthys* Whitley, 1940:243 (a substitute name for *Clastes* Cope, preoccupied in Arachnida).

*Paralepidosteus* Arambourg and Joleaud, 1943:42 (type species *P. africanus* Arambourg and Joleaud, 1943, by monotypy).

*Diagnosis*.—Gars with large laterally-compressed gill rakers that are convoluted on their dorsal edges (Fig. 21), lacking medial toothplates on the first three hypobranchials and ceratobranchials, and reduced numbers of tooth plates on other gill arch elements. *Atractosteus* also differs from *Lepisosteus* in retaining, primitively, an ectopterygoid-premaxillary articulation behind the premaxilla proper, in having the articular socket of the supracleithrum without projecting ridges, and in having enlarged dermopalatine fangs as adults.

*Etymology*.—A compound masculine nominative derived from the Greek *attractos* (=spindle) and Latin *osseus* (=bony).

The following names are considered here as *Atractosteus*, species indeterminate:

†*Clastes pastulosus* Sauvage, 1897:94 (Cretaceous, Portugal).

†*Atractosteus lapidosus* Hay, 1919:110; 1923:375 (? *A. spatula*, Pleistocene, Florida).

†*Atractosteus strausi* (Kinkelin)

Figs. 40-46, 47a, 49a, 51a, 53b

*Lepidosteus strausi* Kinkelin, 1884:244; 1903:25-26. Andraee, 1893:7; 1894:359. Woodward, 1895:444.

*Diagnosis.*—Differs from all *Atractosteus* except *A. tropicus* in that *A. strausi* has sheets of enameloid on the frontals, parietals, dermopterotics, and supratemporals. Differs from *A. tropicus* in having long, continuous enameloid tubercles on the opercular bones, whereas *A. tropicus* has reduced amounts of enameloid on these bones and in having larger scales (lateral line scale count of approximately 45 in *strausi*, 51-56 in *tropicus*).

*Type.*—A series of scales deposited at the Senckenberg Museum, not examined in this study.

*Formation and age.*—Messel Locality, Darmstadt, Germany, Eocene.

*Description and comparisons.*—*Atrac-*

*tosteus strausi* is an Eocene gar attaining large size. A whole specimen (AMNH P.4626) is shown in Fig. 40. A closeup of this skull, two other skulls (AMNH 33839, 33856), and accompanying outline drawings of these skulls are shown in Figs. 41-46. Meristics are shown in Table 2. Morphometrics expressed as proportions of dorsal head length of AMNH P.4626 are shown in Tables 3 and 4.

Premaxilla with two complete rows of teeth. Dermopalatine with an inner row of enlarged fangs. Six infraorbitals, three lacrimals, seven to eight circumorbitals, dorsal circumorbital thin, dermosphenotic included in the orbital margin. Suborbitals large, not as numerous as those of the *spatula* group. Two supratemporals on each side of midline.

Frontal shape typical of the genus, most similar to *A. simplex* (probably a result of similar skull compression, Fig. 53). Shape and enameloid patterns of dermopterotic, parietal, and opercular shown in Figs. 47a, 49a, and 51a, respectively. Enameloid usually in broad, intersecting sheets on dorsal dermal bones, and in long, narrow tubercles on opercular series. Infraorbitals, circumorbitals, and suborbitals with enameloid tubercles. Vertebrae subtriangular, with broad ventral ridges. Scales smooth.

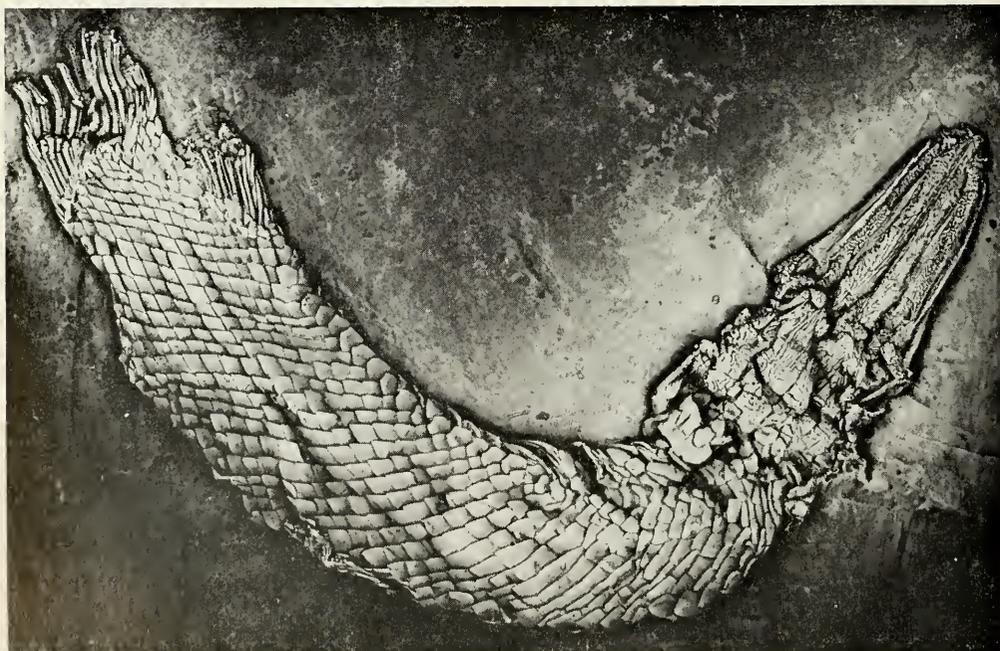
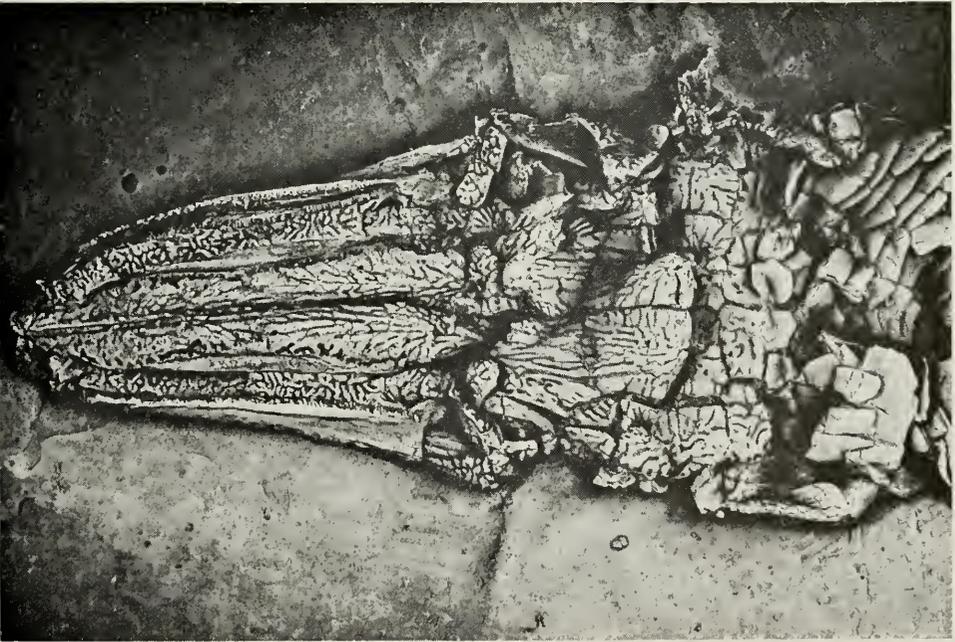
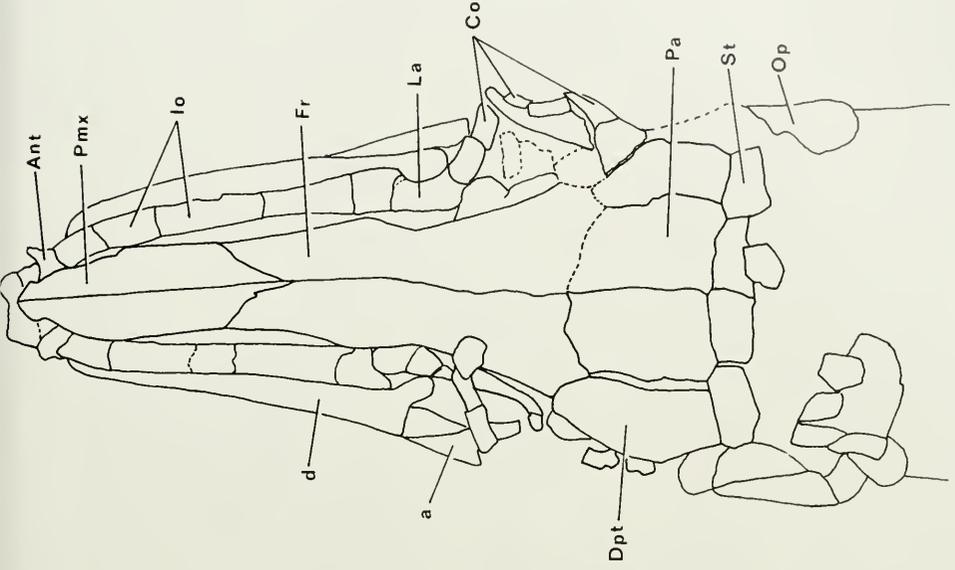
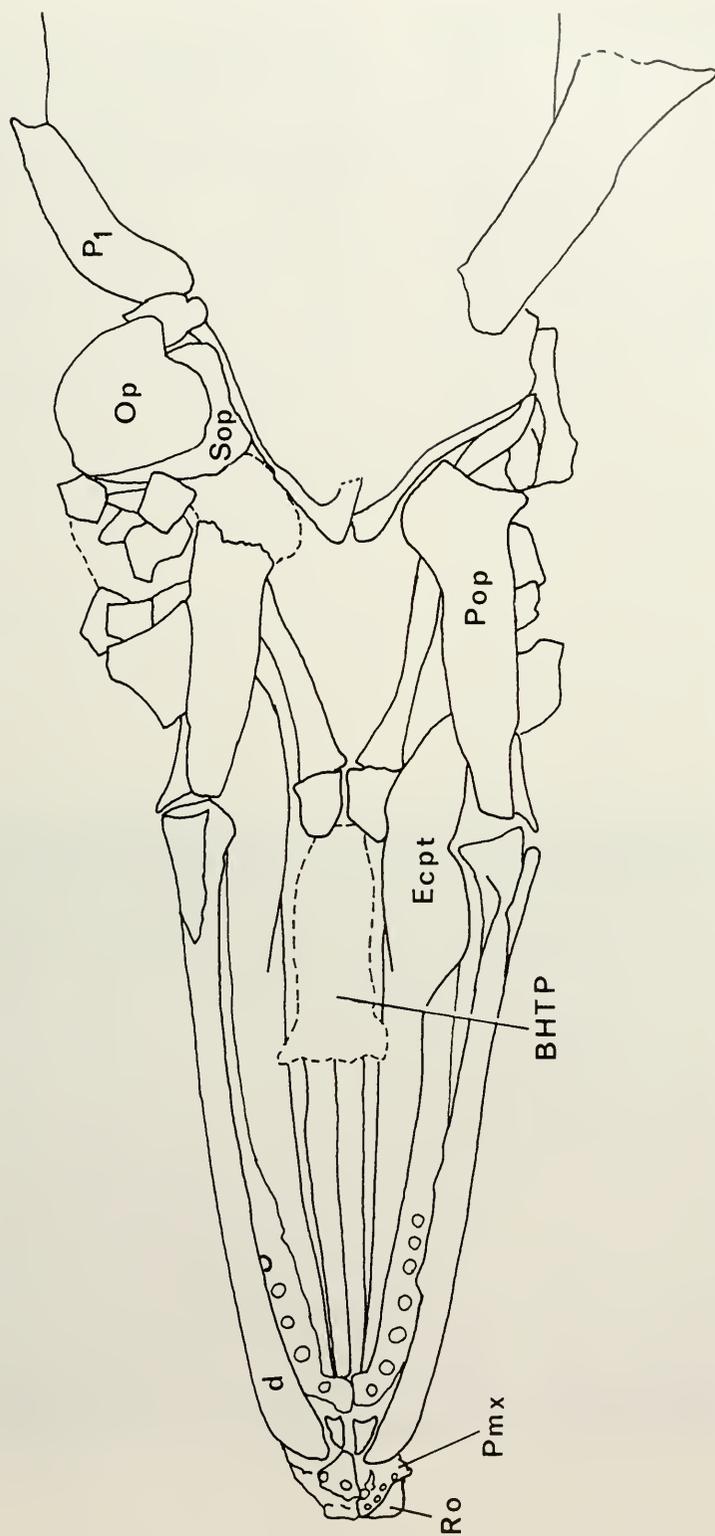


FIG. 40.—Dorsal view of *Atractosteus strausi* (AMNH P.4626, DHL-52.6mm).

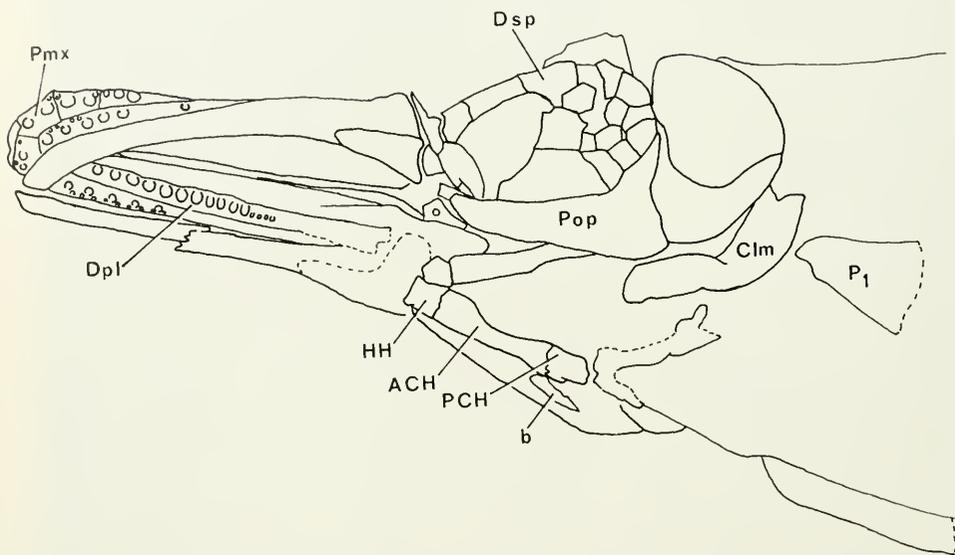


FIGS. 41 and 42.—Dorsal view (left) and outline drawing (right) of the skull of *Atractosteus strausi* (AMNH P.4626, DHL-52.6mm). a, angular; Ant, antorbital; Co, circumorbital; d, dentary; Dpt, dermopterotic; Fr, frontal; Io, infraorbital; La, lacrima; Pa, parietal; Pmx, premaxilla; St, supraorbital.





FIGS. 45 and 46.—Ventral view (left) and outline drawing (right) of *Atractosteus trausi* (AMNH 33856, LLJ-38mm). BHTP, basihyal tooth plates; d, dentary; Ecpt, ectopterygoid; Op, opercular; Sop, preopercular; Pop, pectoral fin; Pmx, premaxillary; Pop, preopercular; Sop, subopercular.



FIGS. 43 and 44.—Lateral view (left) and outline drawing (right) of *Atractosteus trausi* (AMNH 33839, snout to end of opercular-63.4mm).  
 ACH, Anterior ceratohyal; b, branchiostegal; Clim, cleithrum; Dpl, dermosphenotic; HH, hypohyal; P<sub>1</sub>, pectoral fin; PCH, posterior ceratohyal; Pmx, premaxilla; Pop, preopercular.

*Atractosteus trausi* differs from *A. simplex* in that *A. trausi* has three lacrimals and three circumorbitals on the posterior orbital border, whereas *A. simplex* has two lacrimals and two circumorbitals bordering the posterior orbital margin. Also differs from *A. occidentalis*, *A. atrox*, *A. spatula*, and *A. tristoechus* in that *A. trausi* has a narrow dorsal circumorbital that does not exclude the dermosphenotic from the orbital margin and a large orbit, whereas the *spatula* group has a broad dorsal circumorbital which excludes the dermosphenotic from the orbital margin and a small orbit.

*Etymology.*—The trivial name in honor of Herrn Banquier Caesar Strauss.

*Other comments.*—See other comments for *L. fimbriatus*.

### *Atractosteus tropicus* Gill

#### TROPICAL GAR

Figs. 6, 21e, 22b, 47b, 49b, 51a, 54, 55a, 56c

*Atractosteus tropicus* Gill, 1863:172. Duméril, 1870:367. Jordan, Evermann, and Clark, 1930:38.

*Atractosteus belandieri*: Duméril, 1870:368 (Listed as a synonym of *A. tropicus*).

*Lepisosteus tropicus*: Jordan and Evermann, 1896a:111. Miller, 1954:230. Suttkus, 1963:70.

*Diagnosis.*—Differs from all other *Atractosteus* except *A. trausi* in having convoluted sheets of enameloid on the dermal skull roofing bones. Differs from *A. trausi* in having reduced amounts of enameloid on the opercular series (*A. trausi* has numerous elongate tubercles on these bones) and more lateral line scales (see diagnosis of *A. trausi*).

*Description and Comparisons.*—*Atractosteus tropicus* is a small Middle American gar with more body pigmentation than other *Atractosteus*. A skull of typical specimen is shown in Fig. 54.

Juvenile color pattern (based on AMNH 33851, 155 mm specimen): dorsum dark, flank light. Flank stripe as dark as dorsum, not serrate, running from caudal peduncle to eye, there fusing with general head pigmentation. A thin, less pigmented area between flank stripe

and dark dorsum extends from opercular anterior to orbital margin. Paired ventral belly stripes on each side extend from opercular membrane to anal fin, merge, and continue as single stripe to caudal fin. Belly between belly stripes with irregular pigment blotches. Ventral base of pectoral fin and first half of fin rays and membrane dark brown. One additional transverse pigment stripe on pectoral approximately two-thirds the distance from base to tip. Head with distinct retroarticular and preopercular stripes, preopercular stripe extending onto lacrimals. Lower jaw dark except for lightly pigmented area between retroarticular stripe and other darker pigment. Head uniformly dark, without blotches. Some lighter areas along junction of infraorbitals. Gular region with dark stripes along medial jaw margin, irregular pigment blotches between stripes. Pelvic fins with three transverse pigment bars. Dorsal, anal, caudal fins with rays alternately light and dark, but fin membranes with little or no pigment.

In adults, no distinct dorsal stripe; dorsum either uniformly dark or light with numerous brown pigment blotches. Flank stripe continuous only on caudal peduncle, broken into brown pigment blotches anteriorly if specimen has a light dorsum with blotches, or solid brown pigment blotches anteriorly if specimen has a light dorsum with blotches, or solid brown pigment of dorsum extending ventrally to level of ventral margin of flank stripe on caudal peduncle. Flank stripe consolidated on opercular (dark) and suboperculars (light), ending at orbital margin. Occasional individuals with thin reddish-brown vertical stripes on posterior edge of body scales extending vertically from dorsum to belly. No ventral belly stripes or pigment blotches on belly. Base of pectoral fins without pigment. Dorsum of head uniformly dark. Preopercular stripe missing or restricted to posterior half of preoperculum. Retroarticular stripe missing or indistinct. Brown pigment on lower jaw restricted to coronoid process. Pectoral fin without distinct pigment blotches. Pelvic fins without distinct transverse bars, occasionally with diffuse blotch on posterior half of fin. Dorsal, anal, caudal fins with rays dark and membrane light. Occasional membrane pigmentation at base of caudal fin.

Premaxilla without ridges on arm, ectopterygoid articulating with premaxilla proper. Premaxilla with two complete tooth rows. Dermopalatine with two tooth rows, inner row of adults enlarged as dermopalatine fangs. Six to eight infraorbitals. Nine to ten circumorbitals; single dorsal circumorbital not enlarged, dermosphenotic incorporated into orbital margin. Three circumorbitals on posterior orbital border including dermosphenotic. Three lacrimals. Suborbitals not numerous, those of ventral-posterior border larger than internal mosaic.

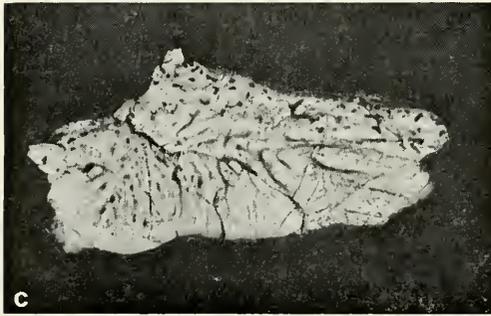
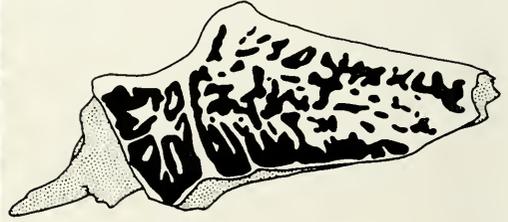
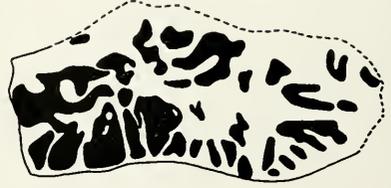


FIG. 47.—Dermopterotics of three *Atractosteus*. (a.) *A. trausi* (AMNH P.4626, 13mm); (b.) *A. tropicus* (AMNH 27939, 29mm); (c.) *A. simplex* (AMNH P.4203, 31mm). Enameloid pattern shown in black on outline drawings; enameloid of c removed from most of the bone.

Two or three supratemporals on each side of midline. Articular facet of supracleithrum without ridges, its shape shown in Fig. 55a.

Dorsal dermal roofing bones with sheets of enameloid. Enameloid reduced on infraorbitals and opercular series. Shapes and enameloid patterns of the dermopterotics, parietals, and opercular shown in Figs. 47a, 49b, and 51b, respectively.

First basihyal toothplate paired. Gill rakers laterally compressed, convoluted on dorsal edge and sitting on basal plates (Fig. 21e). Gill rakers numbering 57-62 on outside of first arch (Table 2). Medial toothplate missing on first three hypobranchials and ceratobranchials and first infrapharyngobranchials, reduced to a single incomplete row on fourth hypobranchials and ceratobranchials and second infrapharyngobranchials (see Fig. 56c).

*Range*.—Río San Juan in Costa Rica, Lake Nicaragua, and Rio Usumacinta Drainage of Guatemala and Mexico; Chiapas, Mexico (Miller, 1954).

*Etymology*.—The trivial name *tropicus* refers to the species' occurrence in Middle America.

*Other comments*.—See comments for *A. spatula* from the Rio Sapoá, Nicaragua and Costa Rica, and from Lake Nicaragua.

#### †*Atractosteus simplex* (Leidy)

Figs. 47c, 49c, 51c, 53c, 55b, 57, 58

*Lepidosteus glaber* Marsh, 1871:105 (name only). Cope, 1874:441 (listed not recog-

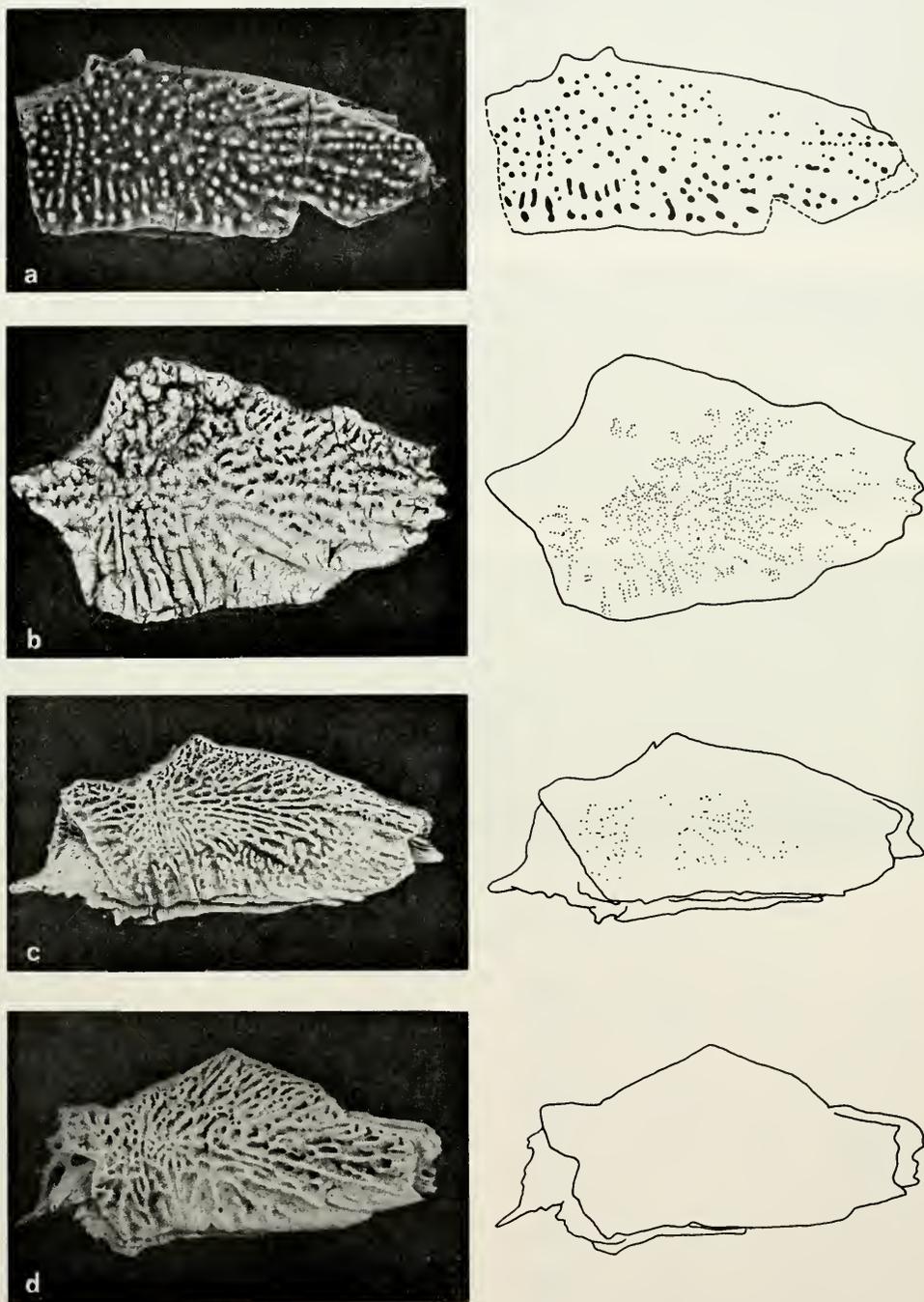


FIG. 48.—Dermopterotics of four *Atractosteus*. (a.) *A. occidentalis* (AMNH P.4304, 37mm); (b.) *A. atrox* (USNM P.4755); (c.) *A. spatula* (TU 388); (d.) *A. tristoechus* (USNM 11309). Enameloid pattern shown in black on outline drawings.

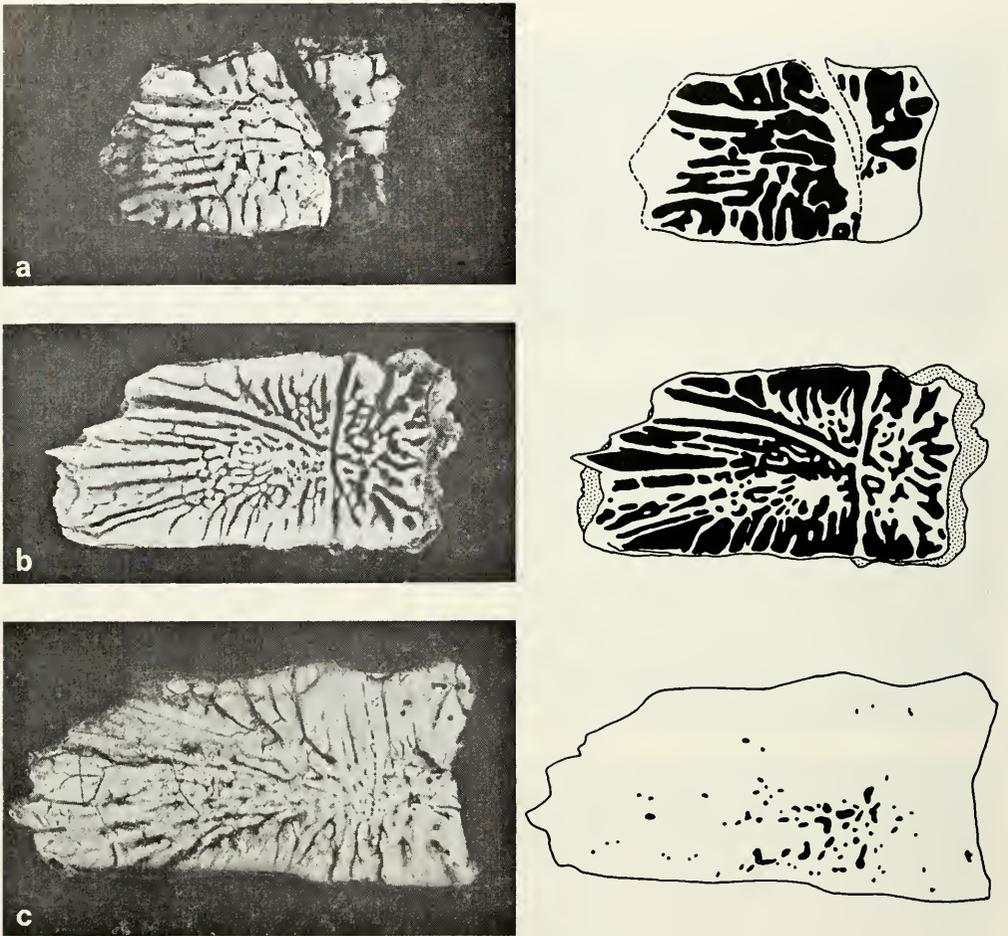


FIG. 49.—Parietals of three *Atractosteus*. (a.) *A. strausi* (AMNH P.4626, 13mm); (b.) *A. tropicus* (AMNH 27939, 25mm); (c.) *A. simplex* (AMNH P.4302, 35mm). Enameloid pattern shown in black on outline drawings; enameloid of c removed from much of the bone.

- nizable). Woodward, 1895:444. Eastman, 1900a:67 (nomen dubium). Cockerell, 1908:163.
- Lepidosteus simplex* Leidy, 1873a:73; 1873b:189. Woodward, 1895:444. Eastman, 1900a:74. Cockerell, 1908:163; 1909:796.
- Clastes glaber*: Cope, 1873:634; King, 1878:376, 405.
- Lepidosteus aganus* Cope, 1877b:40. Cockerell, 1908:163.
- Clastes integer* Cope, 1877b:41. Merrill, 1925:361.
- Lepidosteus glaber*: Hay, 1902:377; 1929:708.
- Lepidosteus simplex*: Hay, 1902:377; 1929:708. Hussarkof and Bryant, 1919:195.
- Lepidosteus aganus*: Hay, 1902:377; 1929:708. Stromer, 1925:361.
- Lepidosteus integer*: Hay, 1902:377; 1929:708.
- Clastes aganus*: Merrill, 1907:7.

*Lepidosteus integer*: Loomis, 1907:358. Cockerell, 1908:163. Stromer, 1925:361.

**Diagnosis.**—Differs from *A. atrox* in having a low, bony ridge on the dermal skull roofing bones overlain by round or slightly elongate enameloid tubercles, whereas *A. atrox* has high bony ridges that are transversely grooved. *Atractosteus simplex* differs from all other *Atractosteus* (for which the characters are known) in having only two lacrimals and two circumorbitals bordering the posterior orbital margin, including the dermosphenotic. *Atractosteus simplex* differs from *A. strausi* and *A. tropicus* in having the dermal skull bone patterns

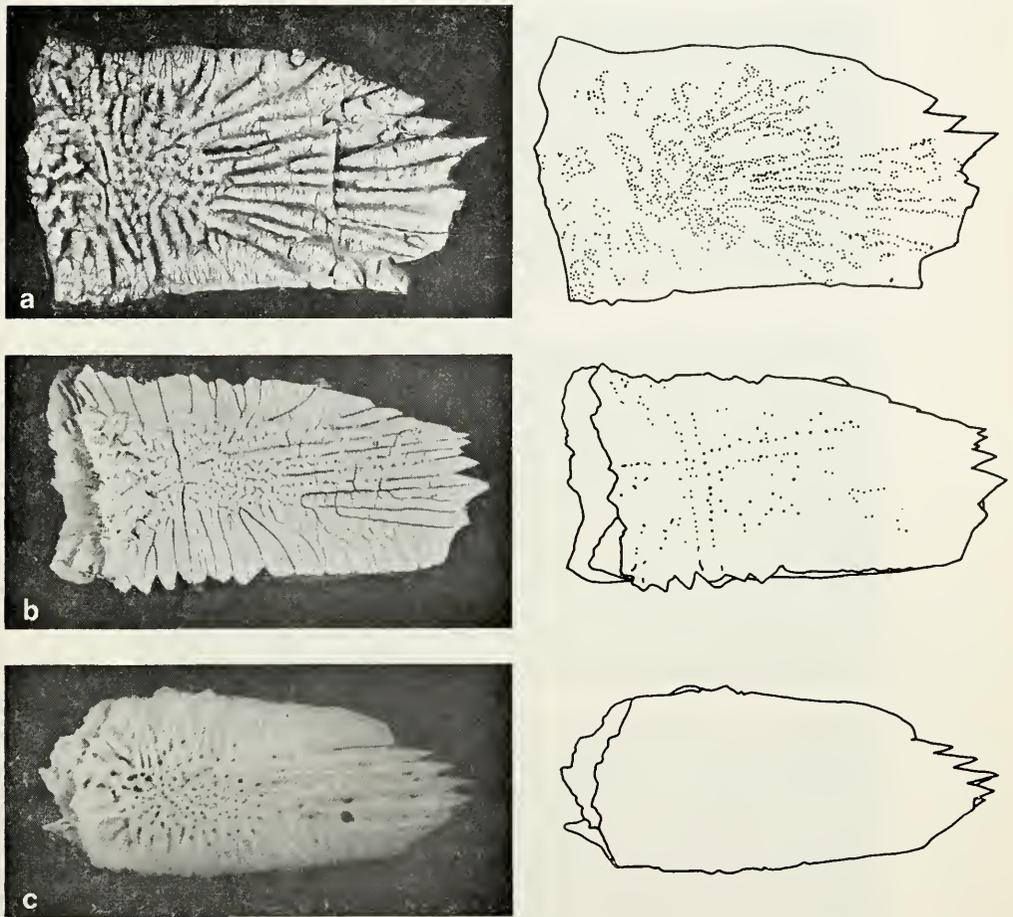


FIG. 50.—Parietals of three *Atractosteus*. (a.) *A. atrox* (USNM P.4755, 39mm); (b.) *A. spatula* (TU 388, 65mm); (c.) *A. tristoechus* (USNM 111308, 50mm). Enameloid pattern shown in black on outline drawings.

described above, whereas *A. tropicus* and *A. strausi* have sheets of enameloid. *Atractosteus simplex* differs from *A. occidentalis*, *A. atrox*, *A. spatula*, and *A. tristoechus* in having the dermosphenotic incorporated into the orbital margin, whereas the other species have an enlarged dorsal circumorbital excluding the dermosphenotic from the orbital margin and in that *A. spatula* has minute, round enameloid tubercles and *A. tristoechus* lacks enameloid and *A. simplex* has larger rounded tubercles.

*Types*.—USNM P.2174, one basioccipital and three vertebrae. USNM P.21173, basioccipital-parasphenoid, three verte-

brae, a tooth, an “antorbital,” and three scales designated cotypes.

*Type locality*.—Junction of the Green and Big Sandy rivers, Sweetwater County, Wyoming.

*Formation and Age*.—Bridger, Watsch, and Green River Formations, Lower Eocene.

*Description and comparisons*.—The type and cotype resemble the bones associated with more complete AMNH and USNM specimens. The skull of AMNH P.4302 is shown in Figs. 57 and 58. Meristic data of Eastman (1900a) are shown in Table 2. Morphometrics from this skull: DHL—139.6 mm; PS—72.4 mm; PO<sub>r</sub>—54.2 mm; OpW—18.6 mm; LLJ—86.6

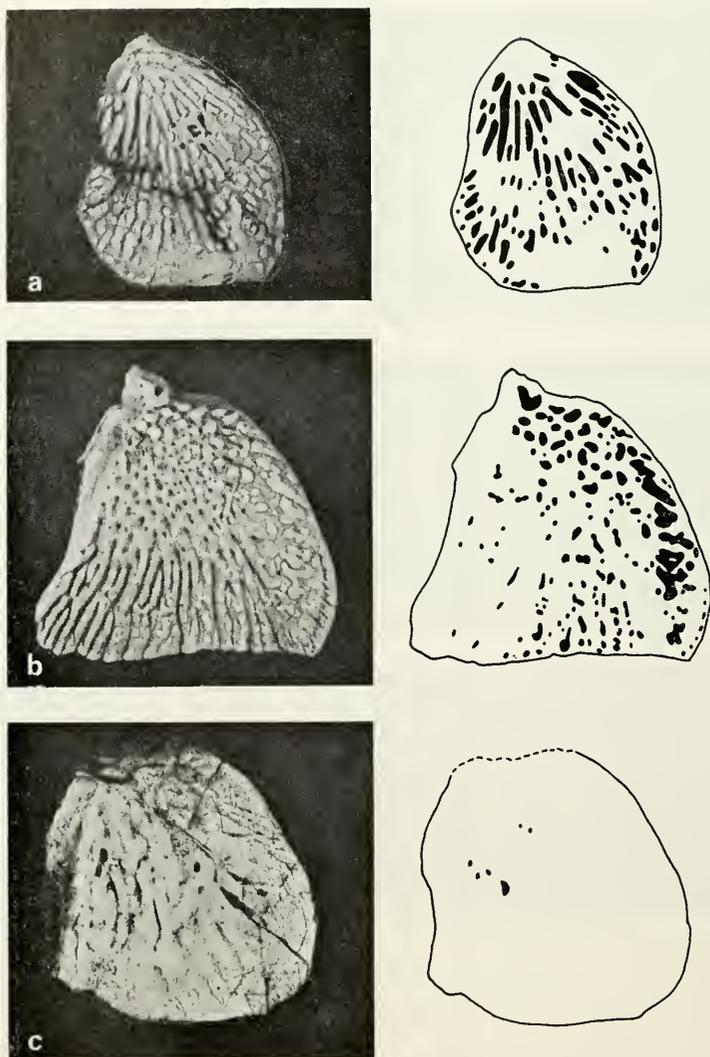


FIG. 51.—Operculars of three *Atractosteus*. (a.) *A. strausi* (AMNH 33839, 12mm); (b.) *A. tropicus* (AMNH 27939, 20mm); (c.) *A. simplex* (AMNH P.4302, 19mm). Enameloid pattern shown in black on outline drawings; enameloid of c removed from most of the bone.

mm; OrD—17.8 mm. Comparisons of these measurements with other gars are shown in Tables 3 and 4.

Two complete rows of premaxillary teeth (USNM P.16712). Dermopalatine has inner tooth row of enlarged dermopalatine fangs (USNM P.16712, AMNH P.4302). Six infraorbitals (AMNH P.4302, P.4308), two lacrimals (AMNH P.4302). Eight circumorbitals (AMNH P.4302), dorsal circumorbital thin; dermosphenotic included in orbital margin. Two circumorbitals make up posterior border of orbit, including dermosphenotic. Relatively few sub-

orbitals; marginal suborbitals bordering preopercular distinctly larger than internal mosaic. Two supratemporals on each side of midline (AMNH P.4302, P.4308). Supracleithrum without distinct projecting ridges above and below articular facet. Supracleithrum shown in Fig. 55b.

Frontal typical of genus (Fig. 53c), most similar to *A. strausi*. Dermopterotic, parietal, and opercular shown in Figs. 47c, 49c, and 51c. Infraorbital enameloid reduced relative to *A. strausi* and *A. tropicus*. Enameloid on other skull roofing bones missing or reduced to small, round or slightly oblong tubercles. Vertebrae

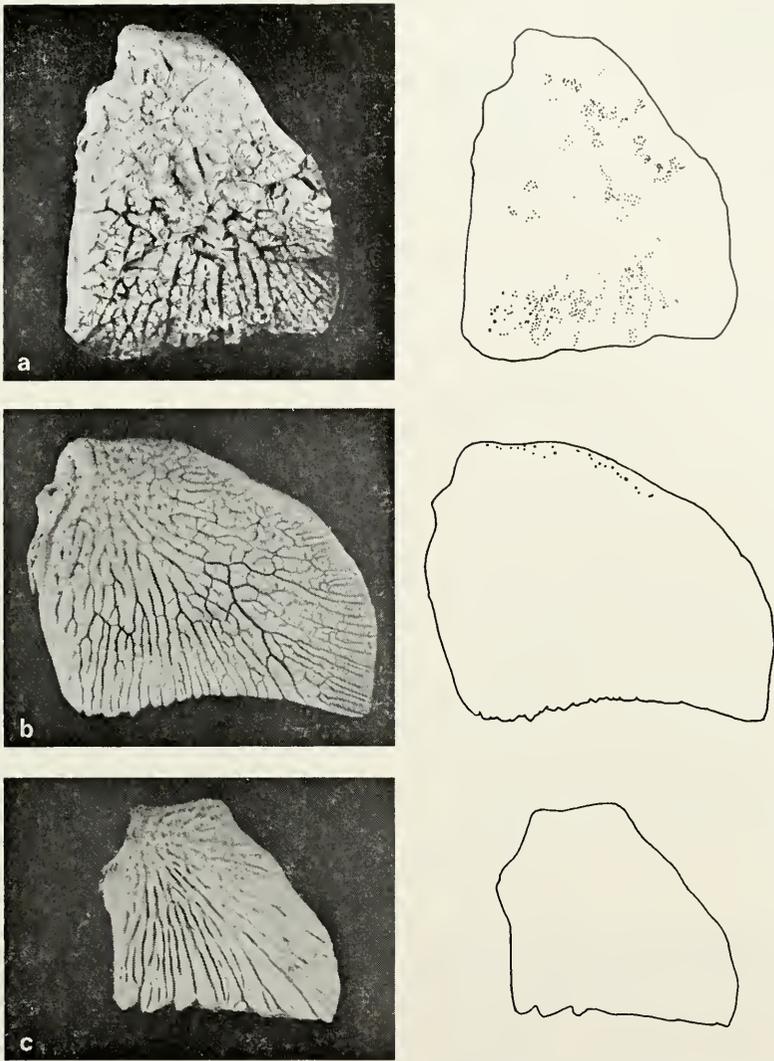


FIG. 52.—Operculars of three *Atractosteus*. (a.) *A. atrox* (USNM P.4755, 43mm); (b.) *A. spatula* (TU 388, 50mm); (c.) *A. tristoechus* (USNM 11309, 30mm). Enameloid pattern shown in black on outline drawing.

of large specimens distinctly subtriangular. Scales smooth.

*Etymology*.—From the Latin, *simplex* (=simple) referring to the smooth scales.

†*Atractosteus africanus* (Arambourg and Joleaud)

Figs. 16, 59

*Paralepidosteus africanus* Arambourg and Joleaud, 1943:42. Casier, 1961:41. Patterson, 1973:295.

*Diagnosis*.—Differs from all other *Atractosteus* in the bony ridge pattern of the one preserved infraorbital (Fig. 16). Vertebrae are larger than other *Atractosteus* but are not diagnosable.

*Type material*.—MHNP N.27-30, N. 155 (vertebrae), N.37 (infraorbital).

*Type locality*.—From the vicinity of Damergou, Niger.

*Formation and age*.—Damergou Beds, Senonian, Upper Cretaceous.

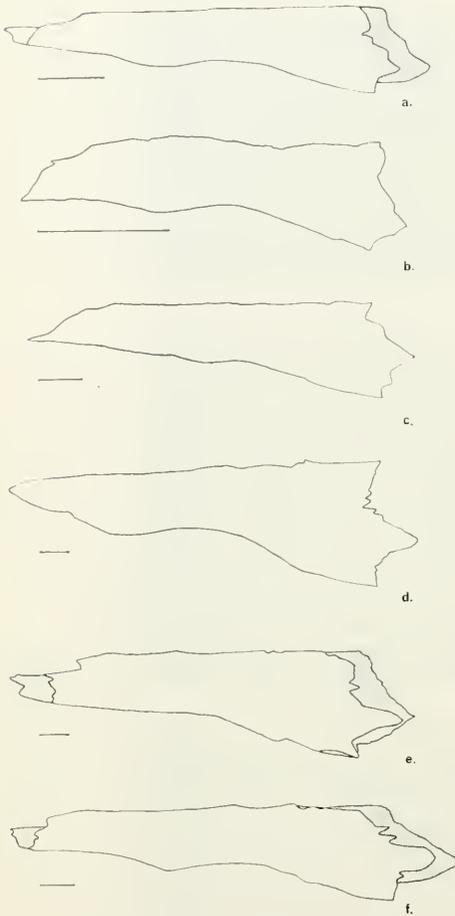


FIG. 53.—Frontal shape of six *Atractosteus*. (a.) *A. tropicus* (AMNH 27870); (b.) *A. strausi* (AMNH P.4626); (c.) *A. simplex* (AMNH P.4302); (d.) *A. atrox* (USNM P.4755); (e.) *A. spatula* (USNM 26166R); (f.) *A. tristoechus* (USNM 111309). A 10mm bar is below each drawing.

*Descriptive comments*.—N.155 a large abdominal vertebra, 41 mm along ventrum of centrum. Transverse processes not preserved, ventral ridges wide, incomplete neural arches. N.27 a large abdominal vertebra (33 mm centrum length, 39.6 mm centrum width, 35.8 mm maximum centrum width), subtriangular, with ventrally directed transverse processes and two widely spread ventral ridges. N.29 a small (13 mm centrum length), almost complete, abdominal vertebra with ventral ridges like N.27. N.28 a posterior abdominal vertebra, with strongly downturned transverse processes, measuring 19 mm in centrum length. N.30 a caudal vertebra, 25 mm in centrum length, with rectangular articulating surface. Infraorbital, N.37,

with a random pitted pattern of dermal ornamentation, not organized into radiating ridges like other *Atractosteus*. This bone interpreted by Arambourg and Joleaud (1943) as part of dentary. Here interpreted as infraorbital, because: (1) in all other *Atractosteus* the last infraorbital has two closely situated rows of outwardly directed teeth, and outer row of teeth not much larger than inner row, a characteristic of N.37; and (2) the infraorbital is flattened like typical posterior *Atractosteus* infraorbitals.

*Etymology*.—The trivial name *africanus* refers to the continent of occurrence.

### †*Atractosteus occidentalis* (Leidy)

Figs. 38c, 48a, 55c, 60

*Lepidosteus occidentalis* Leidy, 1856a:120; 1856b:73. Cope, 1877a:574. Woodward, 1895:126. Lambe, 1902:29; 1904:21, 36, 43. Cockerell, 1908:163.

*Lepidotes haydeni* Leidy, 1856a:120; 1856b:73. Woodward, 1895:125. Hatcher, 1905:67.

*Clastes occidentalis*: Cope, 1884:52.

*Lepisosteus occidentalis*: Cross, 1896:227. Hay, 1902:337; 1903:119; 1910:296; 1929:708. Williston, 1902:953; Matthew, 1916:485. Gilmore, 1924:27. Sternberg, 1924:68. Stomer, 1925:360. Estes, 1964:43; 1969:11.

*Lepisosteus haydeni*: Cockerell, 1908:136.

*Lepidotes occidentalis*: Osborn, 1902:11. Hatcher, 1905:67. Lambe, 1907:179. Peale, 1912:746, 754.

*Diagnosis*.—*Atractosteus occidentalis* differs from *A. strausi*, *A. tropicus*, and *Lepisosteus opertus* in that *occidentalis* lacks enameloid on the infraorbitals, circumorbitals, frontals, and preopercular, and has reduced amounts of enameloid on the dermopterotic, whereas the above three species have enameloid on the infraorbitals, circumorbitals, frontals, and preopercular, and have broad sheets of enameloid on the dermopterotic. Differs from *A. simplex* in that *simplex* has a relatively narrow dorsal circumorbital and a dermosphenotic incorporated into the orbital margin, and low, round or oblong enameloid tubercles on the dermopterotic, whereas *occidentalis* has a thick dorsal circumorbital (which could presumably restrict the dermosphenotic from the orbital margin), and high, rounded enameloid tubercles on the

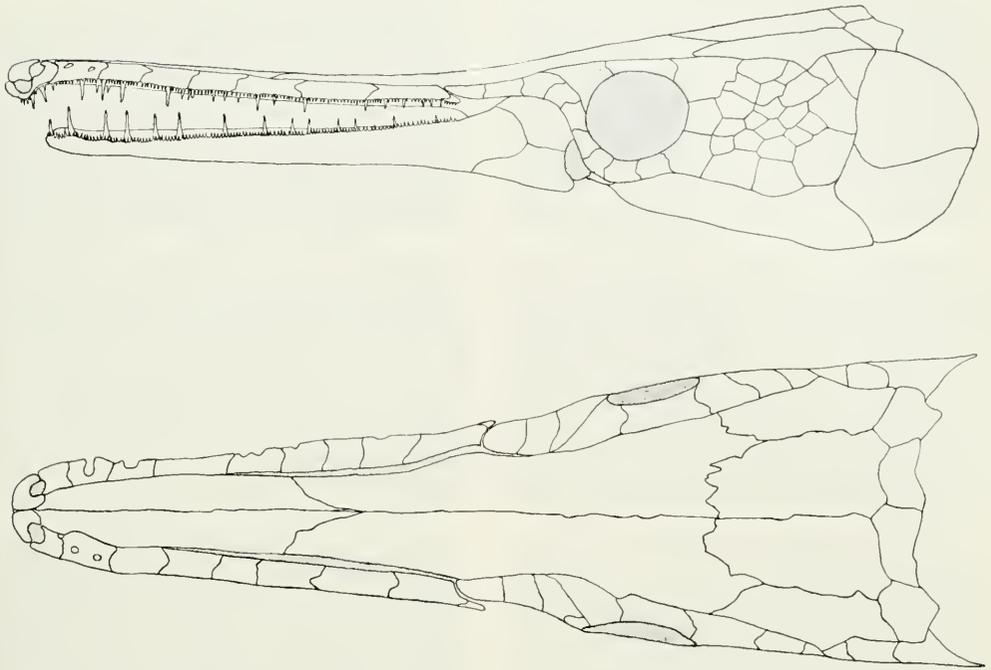


FIG. 54.—Lateral (upper) and dorsal (lower) views of the skull of *Atractosteus tropicus* (AMNH 29075, DHL-123mm).

dermopterotic. Differs from *A. atrox* in that *atrox* has bony ridges that are transversely striated on the frontals and dermopterotics, whereas *occidentalis* has non-striated bony ridges devoid of enameloid on the frontals and low ridges with rounded enameloid tubercles on the dermopterotics. Differs from *A. spatula* in having larger, rounded tubercles, whereas *spatula* has minute, round tubercles. Differs from *A. tristoechus* in that *tristoechus* lacks enameloid, and *occidentalis* has enameloid.

*Type*.—Five scales supposedly deposited at ANSP. I failed to locate the types.

*Type locality*.—Bad Lands of the Judith River, Nebraska Territory. No other locality given.

*Formation and Age*.—Hell Creek, Judith River, Belly River, Lance, and Arapahoe—Denver Formations, Upper Cretaceous.

*Description and comparisons*.—*Atractosteus occidentalis* is known only from disarticulated material. Large premax-

illas from the Hell Creek formation are presumably *A. occidentalis* and have two complete rows of premaxillary teeth (Fig. 38c).

Dermopalatines with enlarged dermopalatine fangs. Infraorbitals almost square, without enameloid. Number of infraorbitals undeterminable but dorsal circumorbital large; presumably excluded dermosphenotic from orbital margin. Those suborbitals that can be distinguished from *L. opertus* small, with few scattered and rounded enameloid tubercles on the bony ridges. Number of supratemporals per side undeterminable. Supracleithrum with simple articular facet, axis of the bone straight. Supracleithrum most similar in shape to *A. atrox* (Fig. 55).

Overall shape of frontal unknown; frontal without enameloid and with low bony ridges. Parietal shape unknown. Shape and enameloid pattern of dermopterotic shown in Fig. 48a. Preoperculum with high bony ridges on the lateral arm, usually devoid of enameloid (Fig. 60). When present, enameloid tubercles on preoperculum minute, widely scattered (1 or 2 per ridge, Fig. 60).

*Etymology*.—From the Latin *occidentalis* (=western).

*Other comments*.—*A. occidentalis* oc-

curs in the same localities as *L. opertus*. Only those bones that can be definitely assigned to *A. occidentalis* are discussed here, and further studies on such bones as the opercular, subopercular, and cleithrum will have to wait the collection of more and better preserved material. The name *A. occidentalis* is applied to the above material because Estes (1964) implied that *A. occidentalis* was close to *A. spatula*.

#### †*Atractosteus atrox* (Leidy)

Figs. 48b, 50a, 52a, 53d, 55d, 61, 62

*Lepidosteus atrox* Leidy, 1873a:73; 1873b:189. Woodward, 1895:445. Eastman, 1900a:57; 1900b:69. Sauvage, 1901:80. Schlosser, 1901:408. Stromer, 1925:360.

*Lepidosteus notabilis* Leidy, 1873a:98; 1873b:192. Woodward, 1895:444.

*Clastes anax* Cope, 1873:634; 1884:53. Merrill, 1907:7.

*Clastes notabilis*: Cope, 1877b:40.

*Clastes atrox*: Cope, 1884:54. Merrill, 1907:7.

*Lepisosteus notabilis*: Hay, 1902:377; 1929:708.

*Lepisosteus atrox* Hay, 1902:377; 1929:708. Jordan, 1905:32. Merrill, 1907:12. Hussakof, 1908:78. Hussakof and Bryant, 1919:195.

*Diagnosis*.—Differs from all other *Atractosteus* in having very thick skull roofing bones that have high bony ridges with transverse striations capped with minute enameloid tubercles.

*Type*.—USNM P.2145, an anterior vertebrae, indistinguishable from other large *Atractosteus* vertebrae.

*Type locality*.—Junction of the Big Sandy and Green Rivers, Sweetwater County, Wyoming.

*Formation and age*.—Bridger Formation, Lower Eocene.

*Description and comparisons*.—A large Eocene *Atractosteus*, distinguished by the enameloid pattern described above. Descriptive comments are based on USNM P.4755 (Figs. 61, 62) and MCZ P.5168 (a complete specimen with crushed skull). Meristics of Eastman (1900a) are shown in Table 2. Morphometrics taken from the USNM P.4755 include: DHL—309 mm; PL—46.6 mm; FL—139.9 mm; PmxL—126.8 mm; OpW—41.5 mm. These measurements, expressed as proportions of dorsal head length are shown in Tables 3 and 4.

Two complete rows of premaxillary teeth. Dermopalatine not observable. Five to six infraorbitals. Number of circumorbitals not determinable. Dorsal circumorbital enlarged, presumably excluded dermosphenotic from orbital margin. Preserved suborbitals small, relative size of marginal suborbitals and internal mosaic not determinable. Three supratemporals on each side of midline. Supracleithrum with simple articular facet, without distinct projecting ridges. Shape of supracleithrum most similar to *A. spatula* and *A. tristoechus* (Fig. 55).

Frontal shape similar to others in genus (Fig. 53d). Shape and enameloid pattern of the dermopterotic, parietal, and opercular shown in Figs. 48b, 50a and 52a. Differs from *A. strausi*, *A. tropicus*, and *A. simplex* in having enlarged dorsal circumorbital excluding dermosphenotic from orbital margin. Differs from *A. spatula* in that *atrox* has enameloid pattern as above, whereas *spatula* has less numerous, larger, rounded tubercles on non-striated ridges. Differs from *A. tristoechus* in that *atrox* has enameloid, whereas *tristoechus* lacks enameloid.

*Etymology*.—From the Latin *atrox* (=savage or hideous).

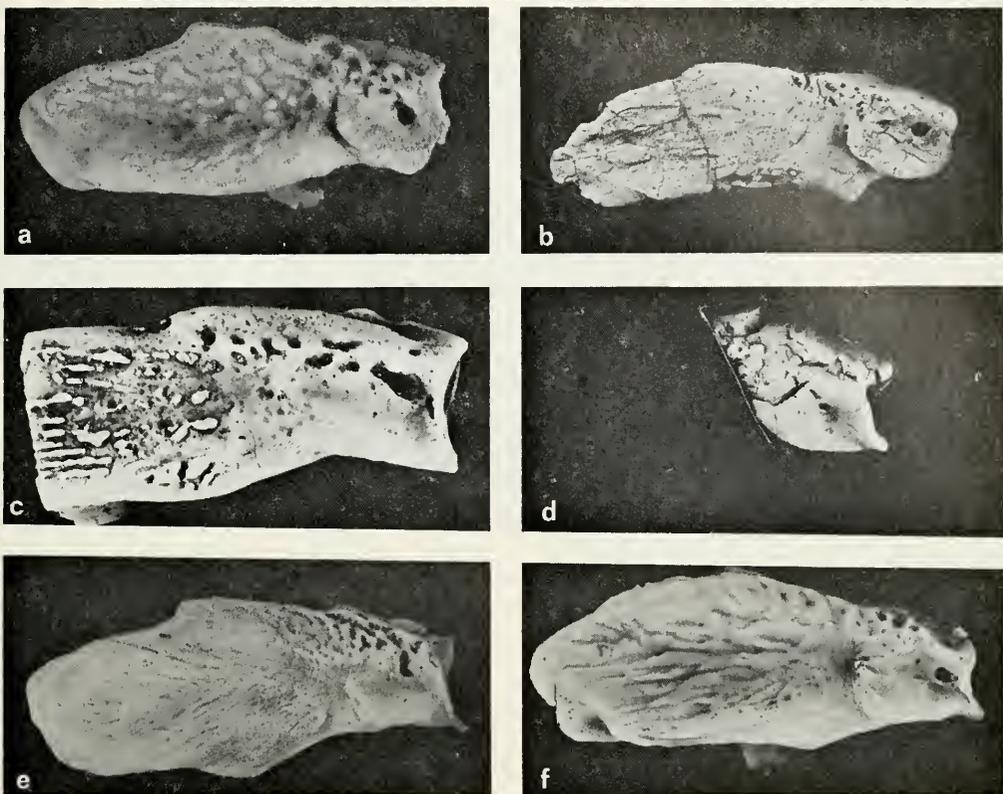


FIG. 55.—Supracleithra of six species of *Atractosteus*. (a.) *A. tropicus* (AMNH 27939, 25mm); (b.) *A. simplex* (AMNH P.4302, 28mm); (c.) *A. occidentalis* (AMNH P.9323); (d.) *A. atrox* (articulatory head only, USNM P.4755, 25mm); (e.) *A. spatula* (USNM 172205R, 55mm); (f.) *A. tristoechus* (USNM 11309, 31mm).

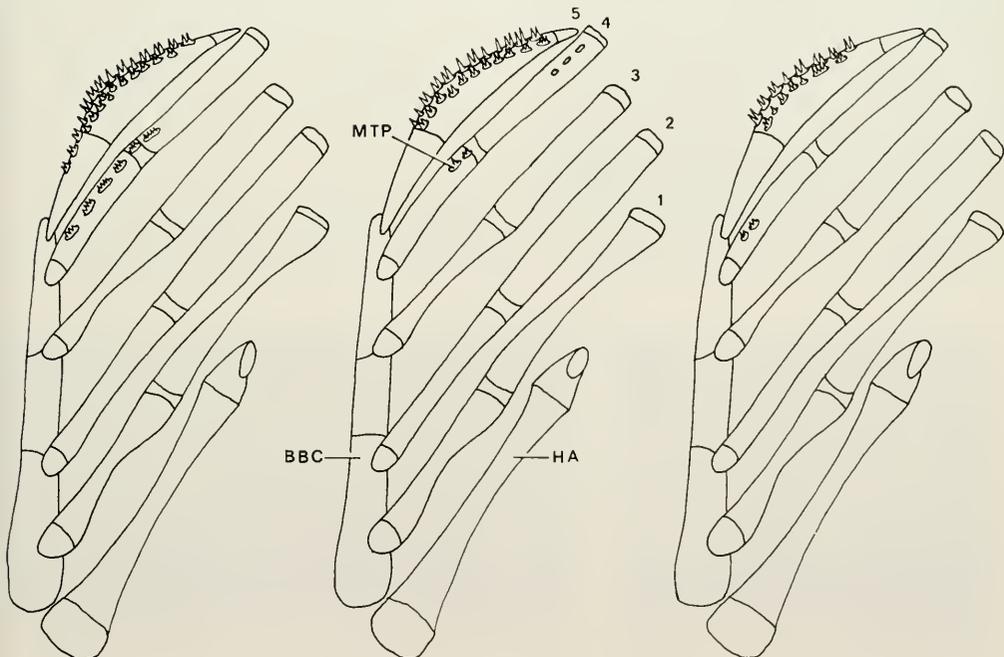
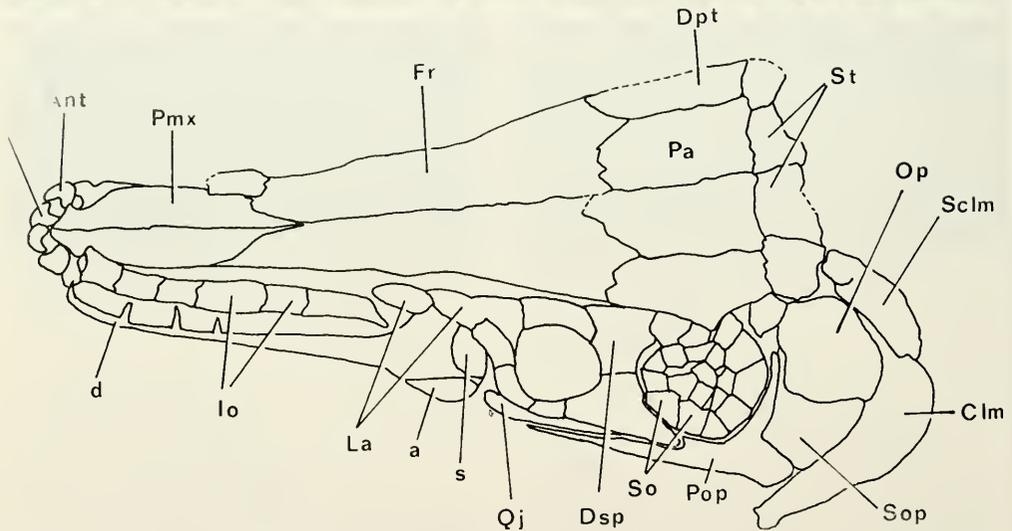
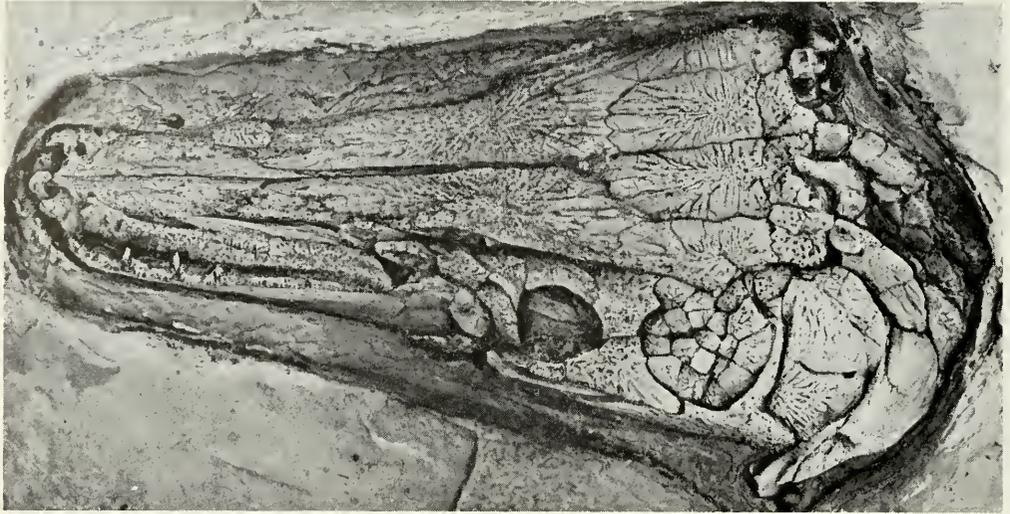


FIG. 56.—Semidiagrammatic dorsal view of the left lower gill arches of three *Atractosteus* gars. Left: *A. tropicus*; middle: *A. spatula*; right: *A. tristoechus*. Gill rakers omitted. BBC, basibranchial copula; HA, hyoid arch; MTP, median toothplates; 1-5, gill arches 1-5.



FIGS. 57 and 58.—Dorsolaterally compressed skull (top) and outline drawing (bottom) of *Atractosteus simplex* (AMNH P.4302, DHL-144mm). a, angular; Ant, antorbital; Clm, cleithrum; d, dentary; Dpt, dermopterygoid; Dsp, dermosphenotic; Fr, frontal; Io, infraorbital; La, lacrimal; Na, nasal; Op, opercular; Pa, parietal; Pmx, premaxillary; Pop, preopercular; Qj, quadratojugal; s, surangular; ScIm, supracleithrum; So, suborbital; Sop, subopercular; St, supratemporal.

TABLE 3.—Range, mean, and standard deviation of four measurements expressed as ratios of dorsal head length for eight species of gars.

| Species                      | N  | SL/DHL             | PS/DHL            | SW/DHL            | LSW/DHL           |
|------------------------------|----|--------------------|-------------------|-------------------|-------------------|
| <i>L. platostomus</i> .....  | 12 | .72-.75 (.74,.01)* | .43-.52 (.47,.03) | .14-.22 (.17,.02) | .09-.12 (.10,.01) |
| <i>L. osseus</i> .....       | 12 | .79-.83 (.81,.01)  | .25-.36 (.33,.05) | .09-.12 (.11,.01) | .04-.06 (.05,.01) |
| <i>L. oculatus</i> .....     | 8  | .70-.77 (.74,.02)  | .33-.52 (.42,.07) | .12-.22 (.18,.03) | .08-.15 (.11,.02) |
| <i>L. platyrhincus</i> ..... | 8  | .69-.83 (.73,.04)  | .33-.53 (.47,.06) | .17-.22 (.19,.02) | .09-.16 (.12,.02) |
| <i>A. tropicus</i> .....     | 32 | .71-.79 (.74,.03)  | .38-.52 (.48,.03) | .18-.26 (.22,.02) | .11-.17 (.14,.02) |
| <i>A. simplex</i> .....      | 1  |                    | .52               |                   | .17               |
| <i>A. spatula</i> .....      | 11 | .69-.75 (.72,.02)  | .48-.62 (.55,.04) | .20-.30 (.27,.04) | .16-.21 (.18,.02) |
| <i>A. tristoechus</i> .....  | 8  | .71-.74 (.73,.01)  | .39-.53 (.47,.07) | .26-.32 (.29,.03) | .17-.20 (.18,.01) |

\* smallest ratio—largest ratio (mean, standard deviation).

*Atractosteus spatula* (Lacépède)

## ALLIGATOR GAR

Figs. 7, 21f, 48c, 50b, 52b, 53c, 55e, 56a, 63

*Lepisosteus spatula* Lacépède, 1803:333. Sutt-  
kus, 1963:83.

*Lepisosteus ferox* Rafinesque, 1820:73. Kirt-  
land, 1844:18.

*Lepisosteus belandieri* Girard, 1858:353.

*Atractosteus lucius* Duméril, 1870:366.

*Lepisosteus viridis* Günther, 1870:329 (not  
*Esox viridis* Gmelin, which is *Lepisosteus*  
*osseus*). Woodward, 1895:441. Goodrich,  
1909:341.

*Litholepis adamantinus* Rafinesque: Jordan,  
1877:16.

*Litholepis spatula*: Jordan, 1877:16.

*Lepisosteus tristoechus*: Jordan, 1885:13 (in  
part, North American populations only).  
Jordan and Evermann, 1896:111. Forbes  
and Richardson, 1920:35 (in part, North  
American populations only).

*Atractosteus spatula*: Jordan, Evermann, and  
Clark, 1930:38.

**Diagnosis.**—*Atractosteus spatula* dif-  
fers from *A. tropicus*, *A. strausi*, *A. sim-  
plex*, and *A. atrox*, in dermal roofing  
bone enameloid patterns (Figs. 47-52),  
from *A. tropicus* in lateral line scale  
count (58-62 in *A. spatula*, 51-56 in *A.*  
*tropicus*), and number of predorsal scales  
(49-54 in *A. spatula*, 43-48 in *A. tropi-  
cus*). *Atractosteus spatula* differs from  
*A. tristoechus* in having enameloid on  
the dermal roofing bones and in gill  
raker count (59-66 rakers on the first  
arch outside row in *A. spatula*, 67-81 in  
*A. tristoechus*).

**Type.**—A mounted specimen depos-  
ited at the Muséum National d'Histoire  
Naturelle, Paris, France.

**Description and comparisons.**—*Atrac-  
tosteus spatula* is the largest of living  
gars reaching a maximum reported  
length of over 3 meters and weight of  
137 kilos (Suttikus, 1963). Meristic  
counts are shown in Table 2. Skull mea-  
surements, as expressions of ratios of dor-  
sal head length, are shown in Tables 3  
and 4. Color pattern descriptions have  
been given by Suttikus (1963) for adults  
and juveniles and by Moore et al. (1973)  
for a small juvenile specimen.

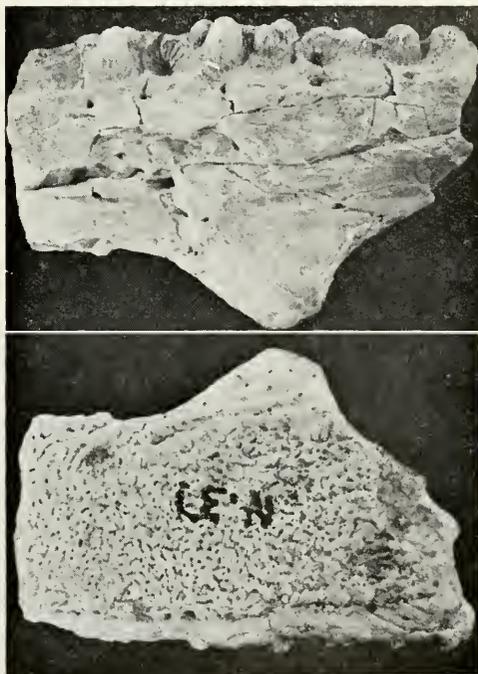


FIG. 59.—Infraorbital (MHNP N.37) of *Atrac-  
tosteus africanus*. Top, dorsal view; bottom,  
ventral view.

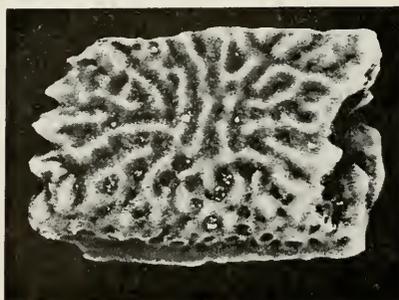
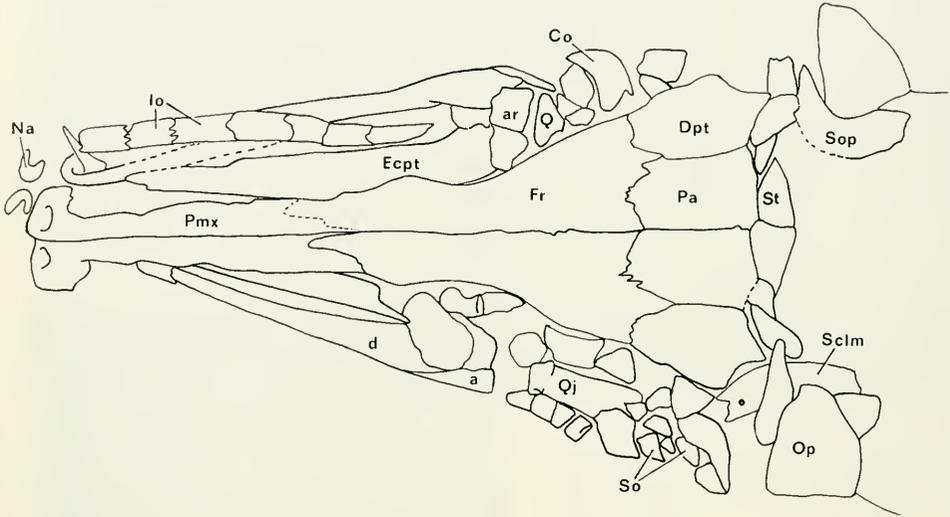


FIG. 60.—Various bones of *Atractosteus occidentalis*. Right, Infraorbital (AMNH P.9323,  
12mm); Left, preopercular (MCZ P.9379, 51mm).



FIGS. 61 and 62.—Dorsal view (left) and outline drawing (right) of the skull of *Atractosteus atrox* (USNM P.4755, DHL-311mm). a, angular; ar, articular; Co, circumorbital; d, dentary; Dpt, dermopteryotic; Ecpt, ectopterygoid; Fr, frontal; Io, infraorbital; Na, nasal; Op, opercular; Pa, parietal; Pmx, premaxilla; Q, quadrate; Qi, quadratojugal; Sclm, supracleithrum; So, suborbital; Sop, supratergular; St, supratemporal.

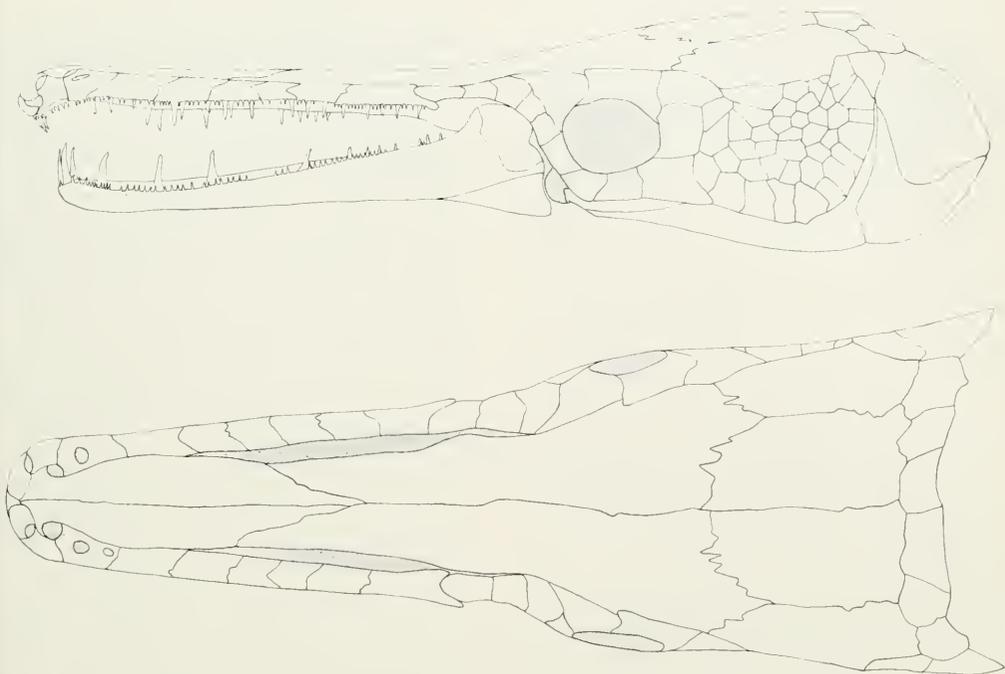


FIG. 63.—Lateral (top) and dorsal (bottom) views of the skull of *Atractosteus spatula* (AMNH 220946, DHL-186mm).

Juveniles with flank stripe, fading with age. Some adults with flank blotches on caudal peduncle. Juveniles and adults without belly stripes, belly without pigment blotches. Head of juveniles dark, no head blotches. Juveniles with pair of dark dorsal stripes bordering a medial light stripe, these stripes running from back of head to base of caudal fin, fading with age. Fins of juveniles with pigment blotches; some adults with blotches. Fin rays usually brown. Adults with dark brown to tan dorsum, fading ventrally to white or yellowish belly. Throat region speckled.

Premaxilla with two complete rows of teeth. Dermopalatine fangs as large as infraorbital fangs in adults. Vomer with single, enlarged fang. Five to seven infraorbitals, with enameloid lost or reduced to a few minute blisters on the bony ridges. Remaining skull roofing bones with minute rounded enameloid tubercles. Opercular series with little or no enameloid. Approximately eight circumorbitals. Dermosphenotic excluded from orbital margin. Many suborbitals; approximately 10 or more along posterior border, including the "dermo-hyals." Three supratemporals on each side of midline (a total of six). Supracleithrum without projecting ridges above and below the articular socket, most similar to that of *A. tristoechus* in shape (Fig. 55e).

Vertebrae of large adults subtriangular in shape, with wide ventral ridges. Anterior scales with ridges, posterior scales smooth.

Gill rakers ornate, sitting on basal plate and laterally compressed (Fig. 21f). Medial toothplates missing on first three arches, reduced to single incomplete row on fourth arch and 3-4 rows on fifth ceratobranchial (Fig. 56a); first basihyal toothplates fused.

*Etymology*.—From the Latin *spatula* (=broad piece or spoon), referring to the broad snout.

*Range*.—From Veracruz, Mexico, northward to the Mississippi River drainage, including the lower reaches of the Ohio and Missouri rivers, and eastward along the Gulf coast to Choctawhatchee Bay, Florida. Also known from the mouth of the Rio Sapoá, Rivas Province, Nicaragua (TU 388) and, based on identifications made by Dr. W. A. Bussing (Universidad de Costa Rica), from Lake Nicaragua and the Rio Sapoá at La

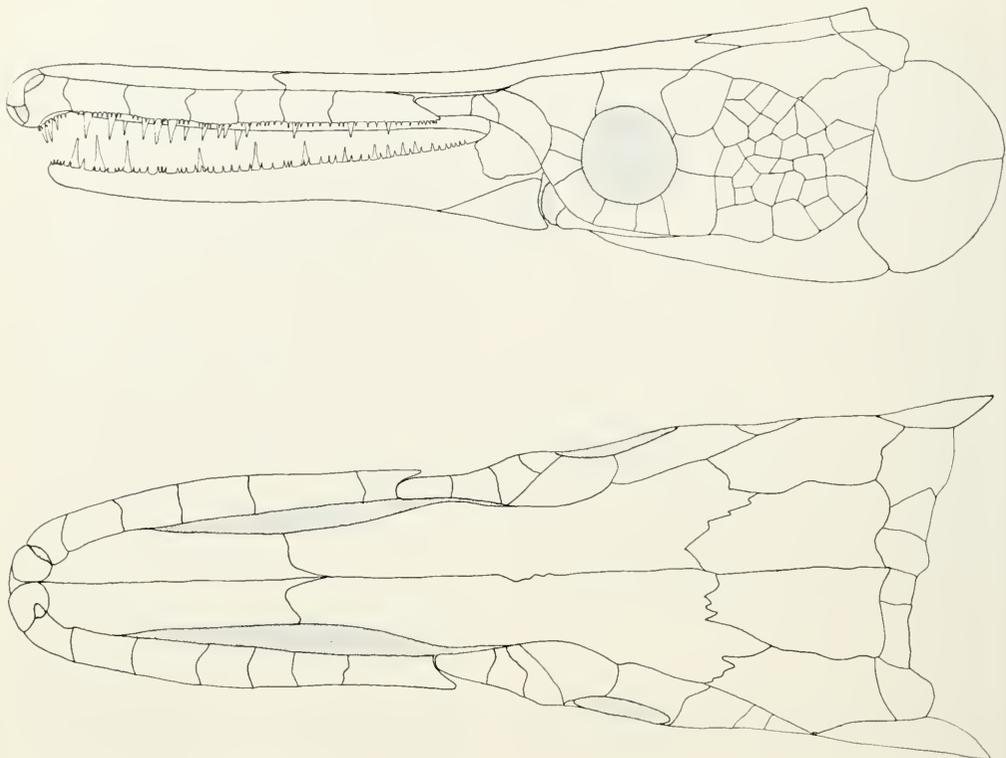


FIG. 64.—Lateral (top) and dorsal (bottom) views of the skull of *Atractosteus tristoechus* (AMNH 3097, DHL-145mm).

Cruz, Guanacaste Province, Costa Rica. Occurrence of this species between the two disjunct populations is unknown.

*Other comments.*—*Atractosteus spatula* has been reported from the lower Pliocene of Kansas (C. L. Smith, 1962) and the Pleistocene of Texas (Hay, 1926; Uyeno and Miller, 1962; Swift, 1968) and Florida (Hay, 1919).

***Atractosteus tristoechus* (Bloch and Schneider)**

**CUBAN GAR OR MANJURAI**

Figs. 5, 48d, 50c, 52c, 53f, 55f, 56b, 64

*Esox tristoechus* Bloch and Schneider, 1801:395.

*Lepidosteus manjuari* Poey, 1854:273.

*Litholepis tristoechus*: Jordan and Gilbert, 1883:92 (in part, Cuban populations only).

*Lepisosteus tristoechus*: Jordan and Evermann, 1896:111 (in part, Cuban populations only).

*Atractosteus tristoechus*: Jordan, Evermann and Clark, 1930:38. Alayo, 1973:11.

*Lepisosteus tristoechus*: Suttkus, 1963:70.

*Diagnosis.*—Differs from all other species of *Atractosteus* in lacking enameloid on the dermal roofing bones of the skull. Differs from all *Atractosteus* except *A. occidentalis*, *A. atrox* and *A. spatula* in having an enlarged dorsal circum-orbital that excludes the dermosphenotic from the orbital margin, from *A. spatula* in gill raker count (67-81 in *A. tristoechus*; 59-66 in *A. spatula*), and from *A. spatula*, *A. occidentalis* and *A. atrox* in lacking enameloid on the skull bones.

*Type.*—Not examined, presumed on deposit with Bloch and Schneider (1801) types at the Humbolt University Museum, East Berlin.

*Description and comparisons.*—A medium-sized *Atractosteus* gar of presumably plain coloration. The skull of a typical specimen is shown in Fig. 64. Meristic data are shown in Table 2. Various morphometric measurements, expressed as ratios of dorsal head length,

are shown in Tables 3 and 4. Specimens examined in this study were old and bleached, but what color pattern remained seemed similar to *A. spatula*.

Premaxilla without ridges on its process, ectopterygoid articulating with premaxilla proper. Two complete rows of premaxillary teeth. Dermopalatine with two tooth rows, inner row enlarged as fangs. Three to five infra-orbitals. Eight to nine circumorbitals; dorsal circumorbital enlarged, excluding demosphentic from orbital margin. Three circumorbitals lining posterior orbital margin, including dorsal circumorbital. Three lacrimals. Sub-orbitals numerous, ventral-posterior marginal suborbitals only slightly larger than internal mosaic. Three or occasionally five supratemporals on each side of midline. Articular facet of the supraclithrum simple, without projecting ridges, devoid of enameloid. Shape of supraclithrum most similar to *A. spatula* (Fig. 55f).

All dermal roofing bones of the skull lacking enameloid. Shape of the dermopterotic, parietals, and opercular shown in Figs. 48d, 50c, and 52c. Frontal shape shown in Fig. 53f.

First basihyal toothplate paired. Gill rakers laterally compressed, convoluted on dorsal edge, sitting on a basal plate (Fig. 21g). Gill rakers numbering 67-81 on first outside arch (Suttkus, 1963; 67-77 on specimens examined in this study). Medial toothplates absent on first three hypobranchials and ceratobranchials and first infrapharyngobranchials (Fig. 56b), reduced to single incomplete row on fourth arch and second infrapharyngobranchials.

*Etymology*.—From the Latin *tri* (= three) and Greek *steachos* (=rows) referring to the rows of teeth of the lower jaw.

*Range*.—Western Cuba and the Isle of Pines.

## PHYLOGENETIC RELATIONSHIPS AMONG GARS

The characters used in the foregoing descriptions of the genera and species of gars are discussed below, along with conclusions concerning their relative apomorphic or plesiomorphic nature. After this discussion, four phylogenetic hypotheses are presented as a summary, two for each genus. The first for each incorporates only the Recent species, whereas the latter two place the fossil morphotypes at the level to which their preserved characters allows. The rationale of this approach rests primarily on the inherent incompleteness of the fossil specimens I examined. I have concluded that the relationships of the fossil forms are best investigated within the context of an understanding of their Recent relatives (following Greenwood et al., 1966; and Nelson, 1969b), for two reasons. First, an analysis based primarily on Recent species is especially desirable (and essential) for gars because many of the major synapomorphies of the two genera are either not preserved in fossils or have not been observed to date in fossils. Other characters, taken in the context of a well corroborated hypothesis of Recent species relationships, and preserved in fossil gars, permit elucidation of relationships of the fossil morphotypes. Thus, much of the analysis of fossil gars concerns the discovery of preservable characters that are correlated

TABLE 4.—Range, mean, and standard deviation of four measurements expressed as ratios of dorsal head length in ten species of gars.

| Species                      | N  | PmxL/DHL          | FL/DHL           | PL/DHL           | LLJ/DHL          |
|------------------------------|----|-------------------|------------------|------------------|------------------|
| <i>L. platostomus</i> .....  | 12 | .41-.53(.48,.03)* | .27-.34(.31,.03) | .20-.23(.22,.01) | .63-.67(.65,.01) |
| <i>L. ossesus</i> .....      | 12 | .52-.64(.58,.04)  | .26-.36(.29,.03) | .12-.18(.15,.02) | .73-.78(.75,.02) |
| <i>L. oculatus</i> .....     | 8  | .35-.52(.44,.06)  | .29-.38(.34,.03) | .16-.23(.20,.03) | .64-.70(.67,.02) |
| <i>L. platyrhincus</i> ..... | 8  | .41-.47(.44,.02)  | .34-.40(.36,.02) | .19-.24(.21,.02) | .61-.67(.64,.02) |
| <i>A. strausi</i> .....      | 1  | .36               |                  |                  | .66              |
| <i>A. tropicus</i> .....     | 32 | .35-.45(.39,.03)  | .34-.45(.41,.02) | .15-.27(.21,.02) | .60-.68(.65,.02) |
| <i>A. simplex</i> .....      | 1  | .33               | .44              | .20              | .62              |
| <i>A. atrox</i> .....        | 1  | .41               | .45              | .15              |                  |
| <i>A. spatula</i> .....      | 11 | .36-.45(.40,.03)  | .34-.42(.38,.02) | .20-.25(.23,.02) | .59-.66(.63,.02) |
| <i>A. tristoechus</i> .....  | 8  | .31-.38(.34,.02)  | .40-.48(.44,.03) | .18-.21(.19,.01) | .63-.72(.73,.01) |

\* smallest ratio—largest ratio (mean, standard deviation).

with synapomorphies of minimal ambiguity.

Beyond these considerations, analyzable fossil gars are rare. In some species, such as *L. opertus* and *A. occidentalis*, the morphotype is represented only by disarticulated remains; many of these remains are not definitely assignable to one or the other species. In *A. africanus* the entire morphotype is represented by one infraorbital and a few vertebrae. In other species, such as *L. indicus* and *A. atrox*, the morphotype is represented by one or two skulls. Because of the small number of specimens available for analysis, intraspecific variation cannot be assessed.

#### MONOPHYLY OF THE GENERA

*Frontal bones.*—The shapes of the frontal bones of all gars reflect the lengthening of the ethmoid and otic regions of the gar snout. As such, the elongate frontals of gars are apomorphous relative to the short snouts of most other actinopterygians. Within the family, the *Atractosteus* gars have shorter frontals (Fig. 53) than the *Lepisosteus* gars (Fig. 20). This is reflected not only in the length of the bone, but also in its articulation with both the premaxillary process and the parietals and dermopterotics. The premaxillary-frontal articulation in *Lepisosteus* is narrow laterally and the posterior arm of the premaxillary process is very thin. In *Atractosteus* the lateral boundary of articulation is broad and slopes gradually toward the posterior of the premaxillary process. In *Lepisosteus* gars the lateral edge of the frontal grows back along the lateral border of the dermopterotic, whereas in *Atractosteus* the dermopterotic and frontal meet at more or less right angles to the long axis of the skull. The narrow and more elongate snout of *Lepisosteus* which is reflected in the shape of the frontal and its articulation with other skull roofing bones is hypothesized to be more apomorphous than the

snout and frontal bone shape of *Atractosteus*.

*Gill Rakers.*—There are two types of gill rakers found among Recent gars. The first, found in *Lepisosteus* gars, is not numerous, is pear-shaped and studded with many relatively large teeth. These gill rakers are similar to those of *Ania calva*, *Albula*, and semionotids (Fig. 21a-d). They are hypothesized to be primitive relative to the gill rakers of *Atractosteus*. The *Atractosteus* gill rakers are numerous, laterally compressed, convoluted on their dorsal edge, and sit on basal plates (Fig. 21e-g). No other actinopterygian is known to have such gill rakers. The *Atractosteus* raker is considered a synapomorphy uniting *Atractosteus* into a monophyletic group.

*Medial toothplates of the visceral arches.*—As discussed above, the dermal arch elements primitively consist of series of lateral plates, gill rakers, and medial toothplates. There are no medial toothplates in *Atractosteus* gars on the hypo- and ceratobranchials of the first three arches and these toothplates are reduced to a single incomplete row on these bones on the fourth arch (Fig. 56). Further, *Atractosteus* gars lack toothplates on the first infrapharyngobranchial and have a reduced number on the second and third infrapharyngobranchials (Fig. 22). *Lepisosteus* gars have these toothplates, albeit reduced as compared with those of other neopterygians such as *Ania* and teleosts (Fig. 34). I conclude that the absence of medial toothplates on the first three arches and a reduction of the fourth arch is a synapomorphy uniting *Atractosteus* gars.

*Ectopterygoid-premaxilla articulation.*—The two genera differ in the way the ectopterygoid and premaxilla articulate with each other. In *Atractosteus*, the ectopterygoid articulates immediately posterior to the nasal foramen on the premaxilla proper. This is essentially the same type of articulation found in other actinopterygians (although, of course, the autapomorphous premaxillary proc-

ess of gars produces a ectopterygoid-premaxillary association not similar to that of other actinopterygians). The articulation in *Lepisosteus* differs in that the ectopterygoid articulates with the premaxillary process and not with the premaxilla proper. In *L. platostomus*, *L. oculatus*, and *L. platyrhincus*, this is reflected by a series of ridges on the premaxillary process (Fig. 38a). In *L. osseus*, the ridges have presumably been obliterated by increased snout length (see discussion below). Unfortunately, no fossil gar has this character preserved. I conclude that Recent *Lepisosteus* gars share a synapomorphic ectopterygoid-premaxilla articulation.

*Dermopalatine fangs*.—During ontogeny the dermopalatines of both *Atractosteus* and *Lepisosteus* juveniles have dermopalatine fangs as large as those on the infraorbitals (Suttikus, 1963). As growth proceeds the dermopalatine teeth of *Lepisosteus* do not grow as large as those of *Atractosteus*. Fully grown *Atractosteus* gars have an inner row of dermopalatine fangs as large as the infraorbital fangs and an outer row of teeth corresponding in size to the outer row of smaller infra-orbital teeth. Adult *Lepisosteus* gars lack the dermopalatine fangs, having only two rows of the smaller teeth. Enlarged dermopalatine teeth are typical of many semionotiforms and of *Amia*. The presence of dermopalatine fangs in outgroups and the ontogenetic evidence leads to a conclusion that the lack of dermopalatine fangs in adult *Lepisosteus* is a synapomorphy of the genus.

*Enameloid*.—Some species of both *Lepisosteus* and *Atractosteus* have broad, flattened enameloid tubercles which interconnect to form convoluted patterns on the parietals and dermopterotics as well as more or less extensive amounts of enameloid on the other skull roofing bones (i.e. *L. opertus*, Figs. 25a, 27a, and *L. cuneatus*, Figs. 25b, 27b; *A. strausi*, Figs. 47a, 49a and *A. tropicus*, Figs. 47b, 49b). In all *Lepisosteus* gars

except *L. indicus* there are also large amounts of enameloid on the infraorbitals and preoperculars (in *L. opertus*, Fig. 23, it is difficult to decide because of weathering). All *Atractosteus* gars show some reduction (or loss) of enameloid on the infraorbitals and the preoperculars or both (Fig. 60). The initial loss, or reduction, of enameloid on the infraorbitals and the tendency toward continued reduction of enameloid on other skull roofing bones is hypothesized here to be apomorphic for the genus *Atractosteus*, whereas the retention of this enameloid in primitive *Lepisosteus* gars is considered plesiomorphic.

*Supracleithrum*.—Gars differ from other actinopterygians in having a supraclithrum with a concave articular facet for articulation with the post-temporal. All *Atractosteus* gars have simple articular facets without bony projections above and below the facets (Fig. 55) while *Lepisosteus* gars have these projections (Fig. 24). The absence of these projections in *Atractosteus* or other actinopterygians leads to a conclusion that the projections are synapomorphic for *Lepisosteus*. The shape of the supraclithrum also differs in the two genera (Figs. 24, 55), but the characterization of either as plesiomorphic or apomorphic is not justified.

#### RELATIONSHIPS AMONG *Lepisosteus* GARS

*Premaxillary tooth pattern*.—The premaxillary teeth are known in six of the eight species of *Lepisosteus*. *Lepisosteus platostomus* and probably *L. opertus* differ from all other species in having two complete rows of teeth on the premaxilla. This is similar to the pattern in *Atractosteus* (Fig. 38c) and is considered plesiomorphic. Other *Lepisosteus* display a reduction trend in the number of teeth on the outer row. *Lepisosteus osseus* has two to four teeth, whereas *L. oculatus*, *L. platyrhincus*, and *L. fimbriatus* (Fig. 38b) have a single tooth on the outer row (occasionally two in *platyrhincus*). The condition in *L. os-*

*seus* is considered plesiomorphous relative to those in the latter three species.

*Ectopterygoid-premaxilla articulation.*—The ectopterygoid-premaxilla articulation is known only from Recent species. The articulation of the ectopterygoid and the nasal process of the premaxilla is considered a synapomorphy of *Lepisosteus* and this articulation is manifested by a series of ridges on the side of the premaxilla in *L. platostomus*, *L. oculatus*, and *L. platyrhincus* (Fig. 38a). *Lepisosteus osseus* does not have these ridges but maintains the usual *Lepisosteus* articulation. It is logical to assume that the loss of ridges on the nasal process in *L. osseus* is an apomorphic condition related to greatly increased snout length in which the ectopterygoid has elongated to such an extent that the bone is very thin at its anterior end.

*Medial toothplates of the gill arches.*—The distribution of medial toothplates is known only in Recent forms. As discussed above, *Lepisosteus* differs from *Atractosteus* in having some medial toothplates on the first three hypobranchials. Both *L. platostomus* and *L. osseus* have medial toothplates on the first hypobranchials, whereas *L. oculatus* and *L. platyrhincus* lack medial toothplates on the first hypobranchials (Fig. 34). This condition in the latter species is hypothesized to be derived relative to the former.

*Color pattern characteristics among Lepisosteus.*—Color patterns vary in adults between very plain (*L. platostomus*) to very spotted (*L. platyrhincus*). Three species, *L. osseus*, *L. platyrhincus*, and *L. oculatus* retain, as adults, more of the juvenile color pattern characteristics common to all Recent species of *Lepisosteus* and to juvenile *A. tropicus*, whereas *L. platostomus* loses or greatly reduces the intensity of these color patterns. The flank stripes, dorsal stripe and belly pigmentation of *L. oculatus*, *L. platyrhincus*, and *L. osseus* are hypothesized to be plesiomorphous relative to the condition found in large juvenile

and adult *L. platostomus* on the basis of ontogenetic and outgroup criteria. The further elucidation of synapomorphies between the other Recent species of *Lepisosteus* is complicated by the range of intraspecific variation found in *L. osseus* and *L. oculatus* (see descriptions above and color notes by Suttkus, 1963). One character seems relatively unambiguous—the large blotches on the head of *L. oculatus* and *L. platyrhincus* are hypothesized to be apomorphic. This hypothesis is weakened by the observation that some *L. osseus* have head blotches (albeit small) while some lack head blotches entirely.

*Enameloid patterns on skull roofing bones.*—As discussed above, the plesiomorphous enameloid pattern for gars is hypothesized to consist of sheets of enameloid on the supratemporals, parietals, and dermopterotics. This pattern is found in *L. opertus* (Figs. 25a, 27a). *Lepisosteus cuneatus* (Figs. 25b, 27b) retains most of the plesiomorphous pattern but shows some reduction of enameloid compared to *L. opertus*. *Lepisosteus oculatus*, *L. platyrhincus*, *L. fimbriatus*, and *L. platostomus* tend to have elongate enameloid tubercles or enameloid tubercles present as series of oblong tubercles on these bones (Figs. 25-28). *Lepisosteus osseus* (Figs. 26a, 28a) has less enameloid on the parietals and dermopterotics than other species, except *L. indicus* (which lacks enameloid completely). All *Lepisosteus* show a tendency to have small rounded enameloid tubercles on the frontal bones (but not *L. opertus*, Fig. 23a, or *L. cuneatus*, Fig. 31). *Lepisosteus osseus* has reduced the amount of enameloid on the frontal bones to a greater extent than other *Lepisosteus* which have enameloid, and the condition in *L. osseus* is hypothesized to be intermediate between the usual condition in the genus and the condition seen in *L. indicus*, in which the enameloid is missing and the bony ridges are reduced in height. The complete loss of enameloid

in *L. indicus* and *A. tristoechus* is considered here as a nonhomology.

*Ethmoid elongation.*—*Lepisosteus osseus* is autapomorphic among Recent species of *Lepisosteus* in the length of its snout. The long snout of *L. indicus* is hypothesized to be a synapomorphy with *L. osseus* when fossil and Recent species are considered (Figs. 20d, e).

#### RELATIONSHIPS AMONG *Atractosteus* GARS

*Dermosphenotic and the circum-orbital series.*—The position of the dermosphenotic, the relative size of the other circumorbitals, and the relative size of the orbit are known in all Recent species of *Atractosteus*, *A. strausi*, *A. simplex*, and can be inferred from the remains of *A. atrox* and *A. occidentalis*. In all of these species except *A. tropicus* (Fig. 54), *A. strausi* (Figs. 41, 42), and *A. simplex* (Figs. 57, 58) the dermosphenotic is excluded from the orbit by an enlargement of the dorsal circum-orbital (the supraorbital) and the orbit is relatively small (Figs. 61, 62, 63, 64). In all Recent and fossil *Lepisosteus* where the condition is known the dermosphenotic is included in the orbital margin, the dorsal circumorbital is thin, and the orbit is large, just as seen in *A. tropicus*, *A. strausi*, and *A. simplex*. I conclude that the conditions seen in *A. tropicus*, *A. strausi*, and *A. simplex* are plesiomorphic relative to that seen in the *spatula* species group.

*Infraorbital enameloid.*—The only two species of *Atractosteus* retaining significant amounts of enameloid on the infraorbitals are *A. tropicus* and *A. strausi*. Other species either completely lack enameloid on the infraorbital or have minute amounts as an individual variation (c.f. *A. spatula*). All disarticulated infraorbitals of *A. occidentalis* examined lacked infraorbital enameloid (Fig. 60a), as do the infraorbitals of the articulated skulls of *A. atrox* and *A. simplex*. The single preserved infraorbital of *A. africanus* lacks enameloid (Fig. 59). Enameloid is present on the infraorbitals of

all *Lepisosteus*, and since large amounts of enameloid on dermal bones seems to be a primitive actinopterygian characteristic, I interpret the presence of infra-orbital enameloid as plesiomorphic. Thus, the lack (or virtual lack) of enameloid in *A. africanus*, *A. occidentalis*, *A. simplex*, *A. atrox*, *A. spatula* and *A. tristoechus* is considered to be derived relative to the condition of *A. tropicus* and *A. strausi*.

*Other enameloid patterns.*—Enameloid patterns within *Atractosteus* include both proliferation and reduction of enameloid. The primitive pattern for the family is hypothesized to be similar to *A. tropicus* and *A. strausi* (as well as *L. opertus*), which have broad, flat, interconnected enameloid tubercles running on top of the bony ridges of the dermopterotics, parietals and other roofing bones (Figs. 47a, b, 49a, b). This hypothesis is not refuted by the observation that many chondrosteans have essentially the same type of enameloid. *A. atrox* has a unique bony ridge pattern and minute enameloid blisters (Figs. 48b, 50a). *Atractosteus occidentalis* and *A. simplex* have reduced numbers of round or oblong tubercles, which are considered to be plesiomorphic relative to the minute enameloid tubercles of *A. atrox* and *A. spatula*. *Atractosteus tristoechus* lacks enameloid completely and is hypothesized to have the most apomorphic condition within this group.

*Color pattern.*—*Atractosteus tropicus* juveniles have all the color pattern characters considered to be plesiomorphic for the family, and adults retain some of these conditions. *Atractosteus spatula* and *A. tristoechus* lack many of these pigment patterns and their color pattern similarities are hypothesized to be apomorphic relative to the patterns of *A. tropicus*.

*Summary of relationships and discussion.*—The four phylograms presented below in Figs. 65-68 represent the least rejected hypotheses of relationships among the species of each genus.

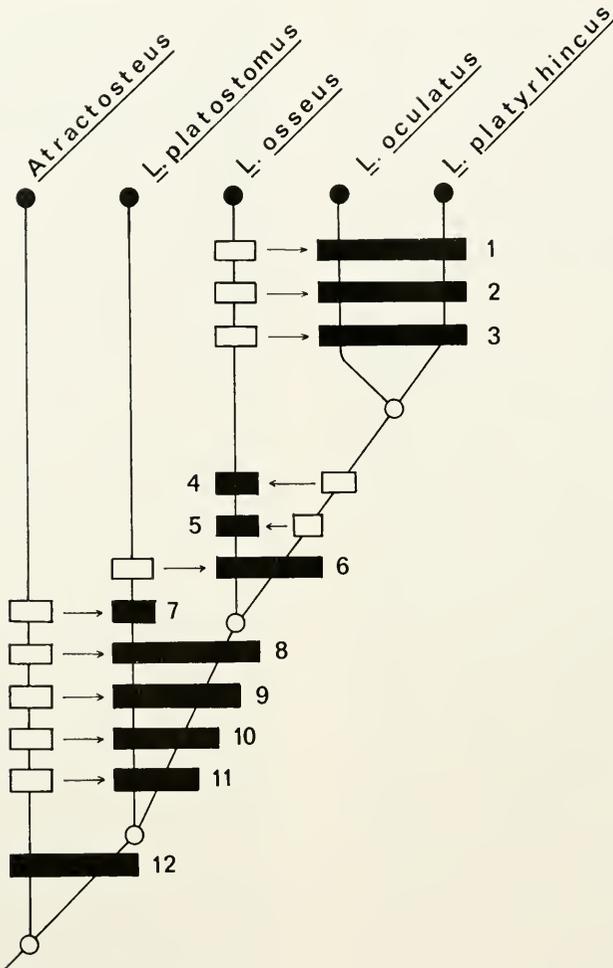


FIG. 65.—Least rejected hypothesis of phylogenetic relationship among recent *Lepisosteus* gars. Synapomorphies (black rectangles) connecting taxa are: (1) large pigment blotches on head; (2) no medial toothplates on first infrapharyngobranchial; (3) single tooth on outer premaxillary tooth row; (4) long narrow snout; (5) ridges on premaxillary arm missing; (6) number of teeth on outer premaxillary tooth row four or less; (7) adults showing a reduction of the primitive color pattern, i.e., no belly stripes, reduced flank stripe, no transverse pigment blotches on paired fins; (8) no enlarged dermopalatine teeth; (9) ecterygoid articulation on premaxillary arm; (10) frontal narrow anteriorly and growing backward posteriorly past the lateral anterior end of the dermopterotic; (11) enameloid on skull roofing bones in narrow elongate tubercles; (12) synapomorphies of the family Lepisosteidae: see Fig. 19.

Fig. 65 is a summary of the least rejected hypothesis of relationships of Recent *Lepisosteus* gars. The monophyly of the genus is corroborated by 4 characters (8-11). That *L. osseus* is more closely related to *L. oculatus* and *L. platyrhincus* is corroborated by one character (6), while the monophyly of the *oculatus-platyrhincus* species pair is corroborated by 3 characters (1-3).

Fig. 66 summarizes the least rejected hypothesis of relationship among fossil and Recent *Lepisosteus*. The only derived character that *L. opertus* shares with other *Lepisosteus* is the correct frontal-dermopterotic articulation. *Lepisosteus cuneatus* has this character, plus a lack of dermopalatine fangs (a condition not observable in *L. opertus*). *Lepisosteus cuneatus* is hypothesized to be

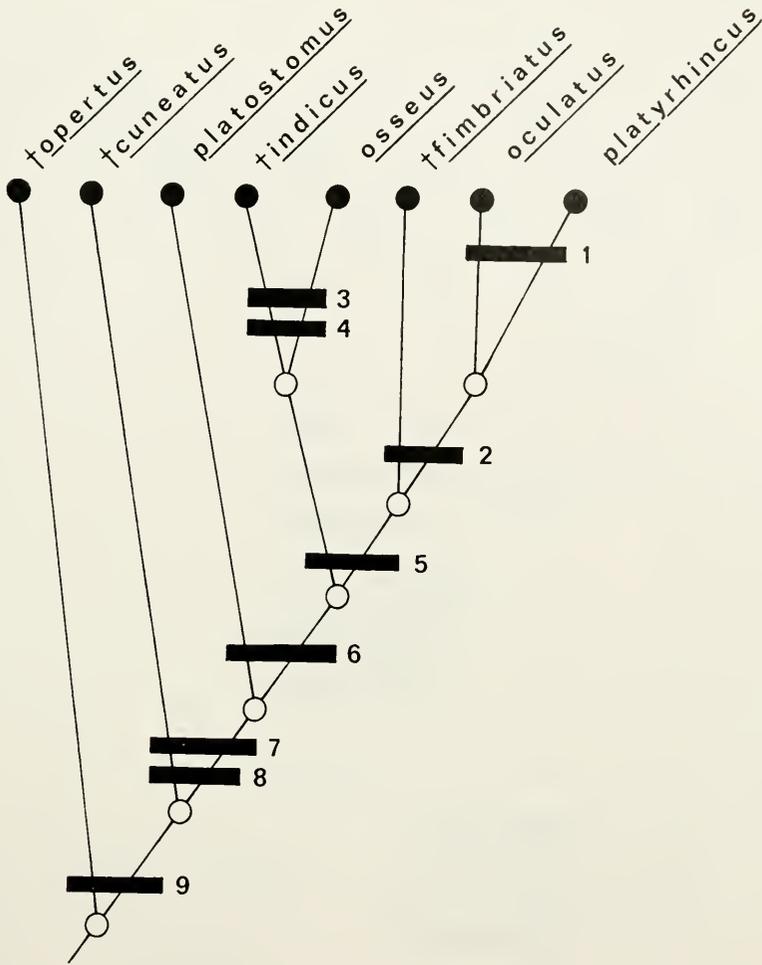


FIG. 66.—Least rejected hypothesis of phylogenetic relationship among fossil and Recent *Lepisosteus*. Synapomorphies (black rectangles) connecting taxa are: (1) synapomorphies 1-3, Fig. 65; (2) single medial tooth on outer premaxillary tooth row; (3) frontal long and narrow anteriorly; (4) enameloid reduced or missing on frontal; (5) number of teeth on outer premaxillary tooth row four or less; (6) enameloid reduced to thin, elongate and/or disconnected tubercles, not in sheets; (7) no dermopalatine fangs; (8) enameloid on skull roofing bones in wide, continuous tubercles, not in sheets; (9) frontal shape of the genus.

more derived than *L. opertus* based on its more derived enameloid pattern. *Lepisosteus indicus* is hypothesized to be the sister species of *L. osseus*, based on the relatively more elongate frontals of both and on the hypothesis that *L. osseus* is intermediate in enameloid pattern and bony ridge height between *L. indicus* and other *Lepisosteus*. *Lepisosteus fimbriatus* is hypothesized to be the sister species of the *oculatus-platyrhincus* species pair, based on the

shared single, medial tooth in the outer tooth row of the premaxillary.

Fig. 67 summarizes the least rejected hypothesis of relationship among Recent *Atractosteus* gars. The monophyly of the genus is corroborated by three synapomorphies (7-9). That *A. spatula* is the Recent sister species of *A. tristoechus* is corroborated by five characters (2-6). One autapomorphy is also presented.

Fig. 68 summarizes the relationship of fossil and Recent *Atractosteus*. *Atrac-*

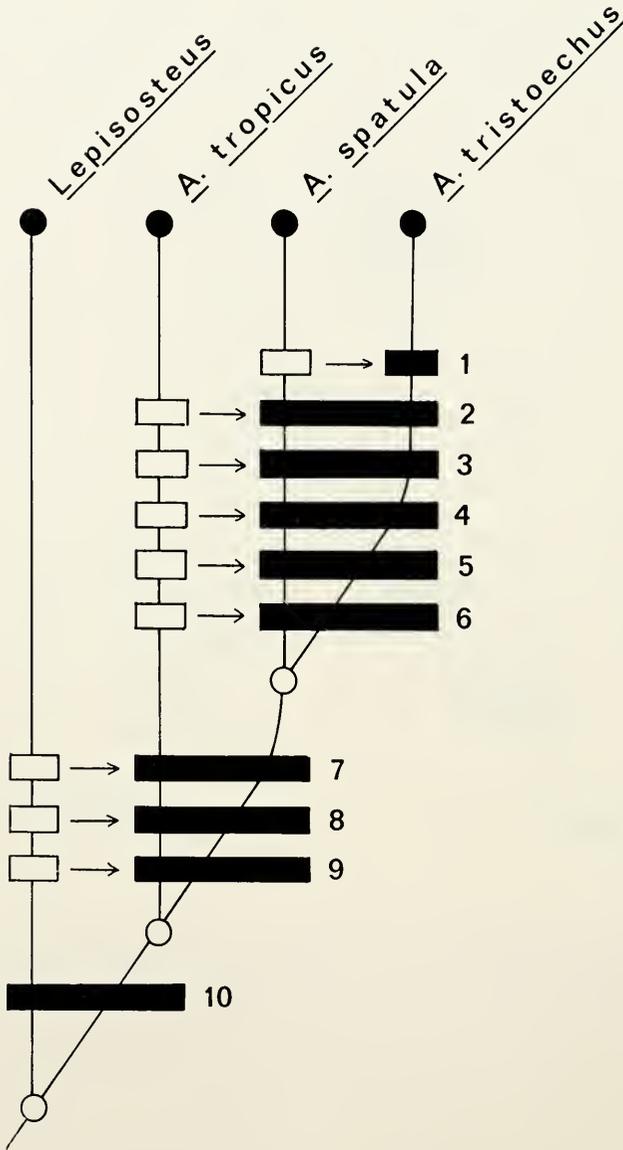


FIG. 67.—Least rejected hypothesis of phylogenetic relationships among Recent *Atractosteus* gars. Synapomorphies (black rectangles) connecting taxa are: (1) No enameloid on skull bones; (2) loss of flank, belly and dorsal stripes in adults; (3) dorsal circumorbital enlarged, dermosphenotic excluded from the orbit; (4) suborbitals numerous compared to other gars; (5) enameloid either missing or reduced to minute, round tubercles on skull roofing bones; (6) no enameloid on infraorbitals; (7) no medial toothplates on first three gill arches ventrally; (8) gill rakers large, laterally compressed, and with basal plates; (9) infraorbital enameloid reduced compared to Recent *Lepisosteus*; (10) synapomorphies of the family *Lepisosteidae*, see Fig. 19.

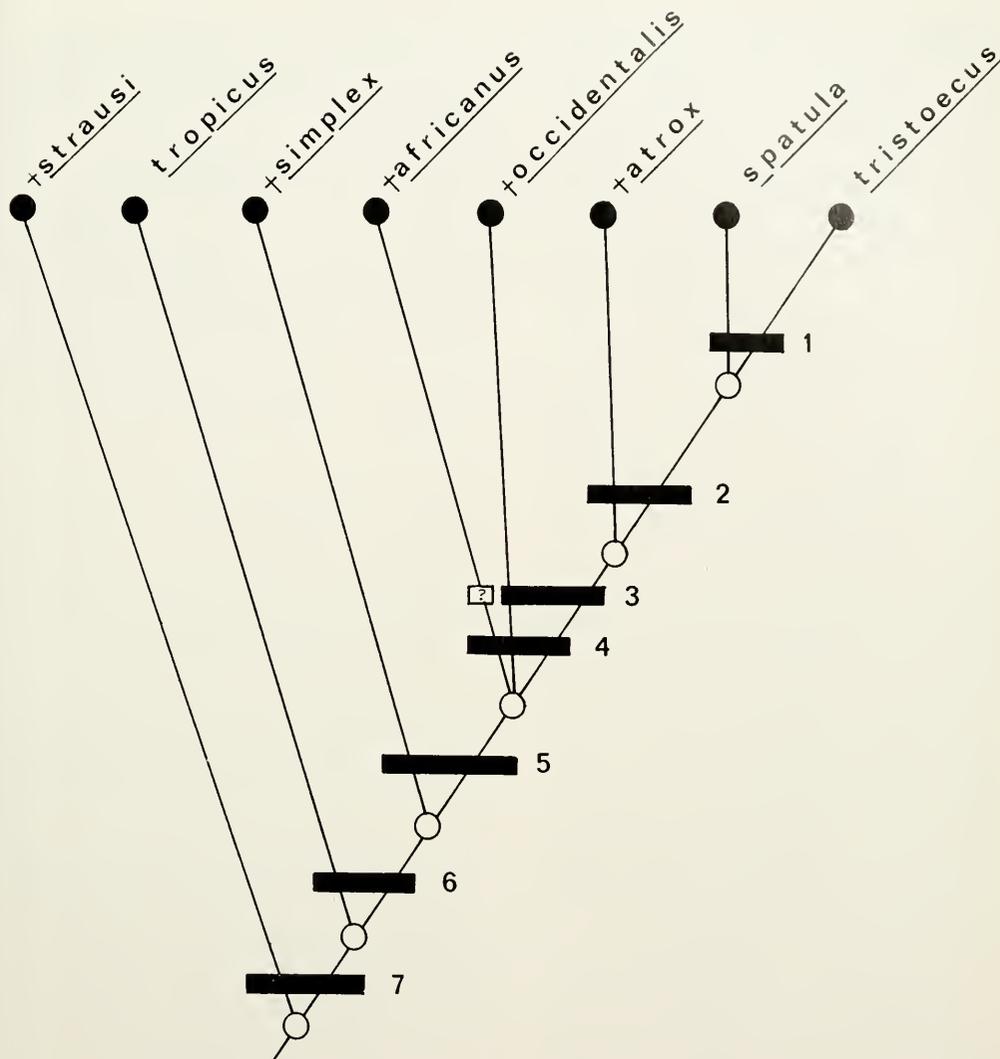


FIG. 68.—Least rejected hypothesis of phylogenetic relationship among fossil and Recent *Atractosteus* gars. Synapomorphies (black rectangles) connecting taxa are: (1) enameloid tubercles missing or minute and not numerous compared to other *Atractosteus*; (2) enameloid tubercles minute but numerous; (3) dorsal circumorbital enlarged (condition of *A. africanus* unknown); (4) no enameloid or virtually no enameloid on infraorbitals; (5) enameloid on dermal skull roofing bones reduced to small, rounded or oblong tubercles, not in sheets; (6) enameloid on opercular bones reduced; (7) enameloid on infraorbitals reduced.

*tosteus strausi* is considered primitive to other *Atractosteus* and its inclusion in the genus is based on reduction of enameloid on the infraorbitals. *Atractosteus tropicus* is hypothesized to be more derived than *A. strausi* based on the reduction of the enameloid tubercles on the preopercular of *A. tropicus* and other *Atractosteus* relative to the retention of

these long enameloid tubercles in *A. strausi*. Other *Atractosteus* either lack enameloid on the infraorbitals or have less enameloid on the infraorbitals than either *A. strausi* or *A. tropicus*. *Atractosteus simplex* is placed above *A. strausi* and *A. tropicus*. *Atractosteus simplex* has a reduction of enameloid on the skull roofing bones but retains the primitive

conditions of a thin dorsal circumorbital and a large orbit (at least in small specimens). *A. africanus* shares with *A. occidentalis* and the other members of the *spatula* species group a severe reduction in infraorbital enameloid (on the one specimen available) and it has subtriangular vertebrae (a similarity produced by growth, i.e., small *A. spatula* have oval centra in cross section, whereas large specimens have triangular centra in cross section). The remaining species (*A. atrox*, *A. occidentalis*, *A. spatula* and *A. tristoechus*) of the *spatula* species group have a large dorsal circumorbital which excludes the dermosphenotic from the orbital margin and have a small orbit relative to the large orbit found in other *Atractosteus* and in all *Lepisosteus*. Within this group *A. atrox* is autapomorphic in having a unique enameloid pattern on the parietals, dermopterotics, and frontals. *Atractosteus occidentalis* is plesiomorphous relative to other members of the group in having large, rounded enameloid tubercles on the skull roofing bones relative to the minute enameloid tubercles found in other species. *Atractosteus tristoechus* is the most derived species based on a complete lack of enameloid in this species.

#### A CLASSIFICATION OF GARS

The classification presented here summarizes the relationship of gars to other actinopterygians and the interrelationships of gars among themselves. This classification adopts two conventions used for combining recent and fossil groups in a single classification, that of Nelson's (1972a, 1973c) use of the term "*incertae sedis*", and that of Patterson's and Rosen's (in press) use of the term "plesion." Nelson (1972a, 1973c) suggested that the term *incertae sedis* be reserved for fossil species or fossil groups of uncertain relationship. These species or groups of species of uncertain position are listed here at the level that their preserved characters allow phylogenetic placement. Patterson and Rosen (in

press) feel the advantage of Nelson's use of the term is that it separates the uncertainties about placement of Recent groups brought about because of deficient theories of relationship from the uncertainties about placement of fossil groups brought about by poor specimen preservation (for example, *A. africanus*). Patterson and Rosen (in press) also used *incertae sedis* for interchangeable taxa and for the inclusion of non-monophyletic groups. Neither of these problems arise in gar classification, and neither connotation is implied by the use of the term here.

The "plesion" (Patterson and Rosen, in press) is a fossil group or a fossil species that is sequenced by a listing convention in a classification and which is the primitive (plesiomorph) sister species (group) of all species listed below it in the classification. Plesions are not given formal rank in the classification presented below. When formal rank is given a plesion, this name is applied only within the context of the classification of the Recent group of which it is a part, and the plesion does not affect the hierarchic position of Recent groups with which it is associated. Thus, if later information is gathered concerning relationships of the plesion, then its position in the classification can be changed without affecting the formal hierarchic ranks of the Recent groups with which it is associated in the classification.

The advantages of this system of conventions can be summarized as (1) uncertainties arising from the incompleteness of fossil specimens are clearly identified in the classification by the term *incertae sedis*, (2) fossil species or groups of species can be incorporated into a classification of Recent organisms without changing the formal ranks of these Recent organisms (thus increasing the information content of the classification over one that included only Recent organisms), (3) the plesion groups can be changed as new information about them is discovered without affect-

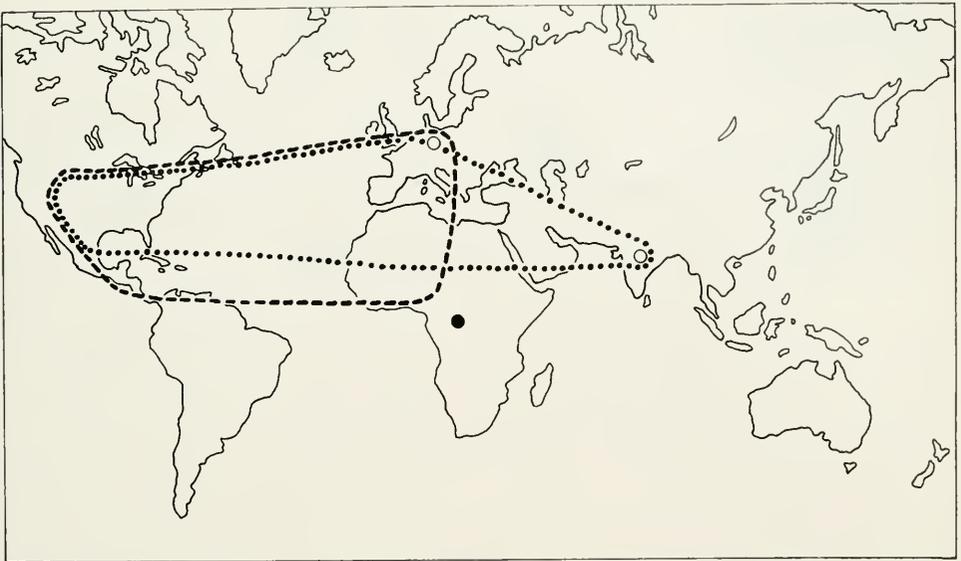


FIG. 69.—Track analysis of the distributional patterns of the genera *Lepisosteus* (dots) and *Atractosteus* (dashes). Black circle is the locality of *Lepisosteidae* species indeterminant (Casier, 1961), which defines the known southern limit of the family in Africa.

ing the ranks of Recent groups, and (4) the phylogenetic relationships among both the fossil and Recent groups can be expressed exactly.

- INFRACLASS **CHONDROSTEI**
- INFRACLASS **NEOPTERYGII**
- DIVISION **HALECOSTOMI**
- SUBDIVISION **HALECOMORPHI**
- SUBDIVISION **TELEOSTEI**
- DIVISION **GINGLYMODI**
- FAMILY **LEPISOSTEIDAE**
- GENUS *Lepisosteus*
  - plesion †*L. opertus*
  - plesion †*L. cuneatus*
  - L. platostomus*
  - L. osseus* species pair
  - plesion †*L. indicus*
  - L. osseus*
  - L. oculatus* species group
  - plesion †*L. fimbriatus*
  - L. oculatus*
  - L. platyrhincus*
- GENUS *Atractosteus*
  - plesion †*A. strausi*
  - A. tropicus*
  - plesion †*A. simplex*
  - A. spatula* species group
  - †*A. africanus* and †*A. occi-*

- dentalis incertae sedis* in *A. spatula* species group.
- plesion †*A. atrox*
- A. spatula*
- A. tristoechus*

GAR BIOGEOGRAPHY

The distribution of gars is analyzed below using the “vicariance” method of analysis discussed in the methods section. Although Recent gars are known only from the northern part of the Western Hemisphere, fossil gars are known from other continental areas (see ranges for the various fossil species above). Of interest here are the distributional patterns, or tracks, of the two genera *Lepisosteus* and *Atractosteus*, and various monophyletic groups of species within each of the genera. These tracks are shown in Figs. 69-72 and are discussed below.

*Distributional patterns of the genera.*—Fig. 69 shows the distributional patterns of *Lepisosteus* and *Atractosteus* projected on a map of present continental positions. The generalized track of *Lepisosteus* includes the ranges of a

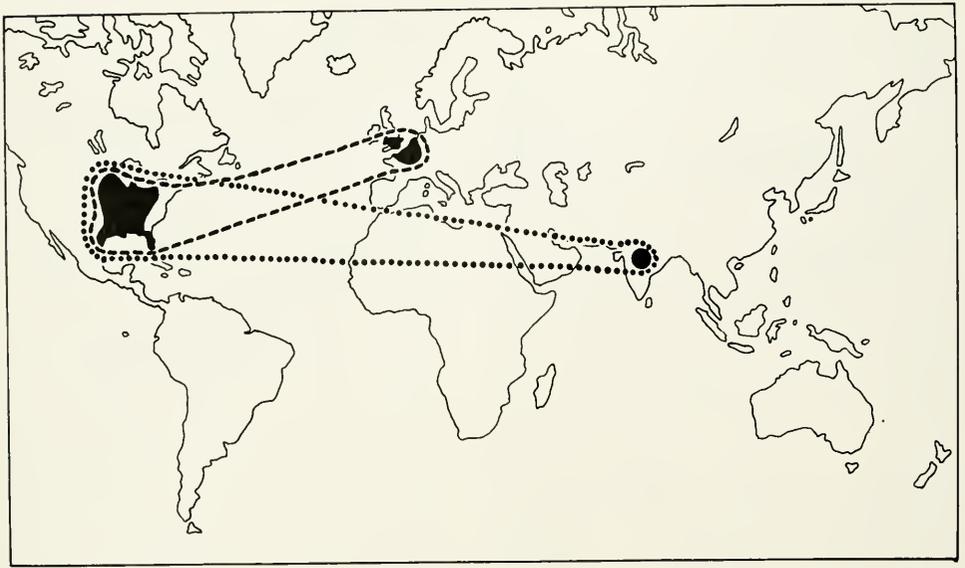


FIG. 70.—Track analysis of the distributional patterns of the *osseus-indicus* species pair (dots) and the *oculatus* species group (dashes). Black areas denote the known range of the *oculatus* species group, black circle denotes the known range of *L. indicus*.

number of species from North America (Upper Cretaceous to Recent), one European species (*L. fimbriatus*, Eocene to Oligocene), and one Indian species (*L. indicus*, Cretaceous). Both northern and southern land masses are included within the track. The *Lepisosteus* generalized track includes three species group tracks within it, and will be examined in a separate section beyond.

The *Atractosteus* generalized track (Fig. 69) includes the ranges of several fossil and one living North American species (Cretaceous to Recent), two nuclear Middle American species (*A. tropicus* and a disjunct population of *A. spatula*), one Caribbean species (*A. tristoechus*), one African species (*A. africanus*), and one European species (*A. strausi*). Like the generalized track of *Lepisosteus*, that of *Atractosteus* includes both northern and southern land masses within its area. The *Atractosteus* generalized track is composed of several individual tracks that will be discussed below in a separate section.

Two observations can be made from the tracks of the two genera: firstly,

both genera are found on parts of what once were Laurasian and Gondwanian land masses; secondly, the genera show a large amount of sympatry, both on Recent and fossil distributions. Three conclusions can be drawn: (1) both genera may have had ancestral Pangean distributions; (2) because sympatry implies dispersal, one or both of the genera must have dispersed (possibly over a Pangean landscape rather than a landscape of present continental positions); (3) because an allopatric speciation event (a vicariance event) must come before dispersal producing sympatry, the vicariance event producing the two genera may have occurred before the break-up of Pangea. Thus, the minimum age of the genera of gars is hypothesized here to be 180 million years before the present.

*Lepisosteus species distributional patterns.*—*Lepisosteus* contains a number of individual tracks. The more primitive members of the genus, *L. opertus* and *L. cuneatus*, are western North American forms, whereas the other members of the genus are either eastern North Ameri-

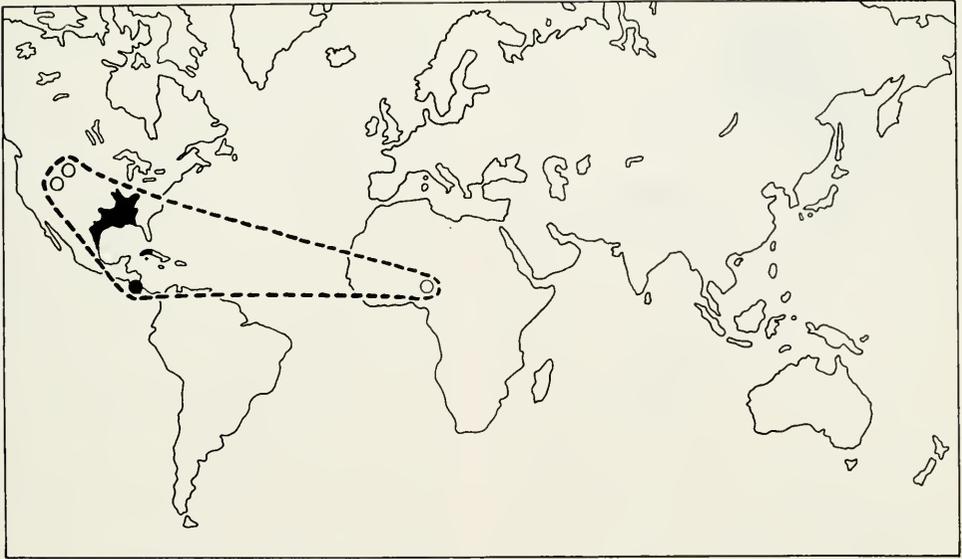


FIG. 71.—Track analysis of the distributional patterns of the *A. spatula* species group, open circles are fossil localities, black areas are Recent species ranges. Black circle is the disjunct population of *A. spatula* from Nicaragua and Costa Rica.

can, European, or Indian. Whether the western ranges of the primitive members of the genus represent an early vicariance event or two early vicariance events is problematical, because it is difficult to determine whether their ranges are the result of sample error in collecting, availability of suitable formations, or whether their observed ranges are representative of their natural ranges. This problem could be resolved by tying these two species to fossil biotas and showing that they form part of a generalized track among Cretaceous and Eocene faunas in general (the same problem exists in determining the biogeographic importance of the western North American fossil *Atractosteus*).

The track describing the range of the group made up of *L. platostomus* and more derived species is identical with that describing the range of the *osseus* species pair plus the *oculatus* species group. This is because *L. platostomus* is found within the range of *L. osseus*. However, it is interesting to note that *L. platostomus* is a relatively westerly form. The *osseus* species pair track (Fig.

70) contains two species, *L. osseus* of North America and *L. indicus* of India (Cretaceous). This track is hypothesized to be older than the *oculatus* species group track because it indicates Pangean distribution. The *oculatus* species group track (Fig. 70) contains two North American species (*L. oculatus* and *L. platyrrhincus*, both Recent) and one European species (*L. fimbriatus*, Eocene to Oligocene). This track conforms to a more generalized track between Europe and eastern North America composed of a number of fossil and Recent groups (McKenna, 1975), and the vicariance event that split the common ancestor of *L. fimbriatus* and *oculatus-platyrrhincus* is hypothesized to be Early Eocene in age.

*Atractosteus species group distributional patterns and Rosen's hypothesis of Caribbean biogeography.*—Rosen (1975) reviewed the biotic composition of the Caribbean region and concluded that several generalized tracks composed of many diverse organisms were involved in producing the distributional patterns appearing in the region today. Two of

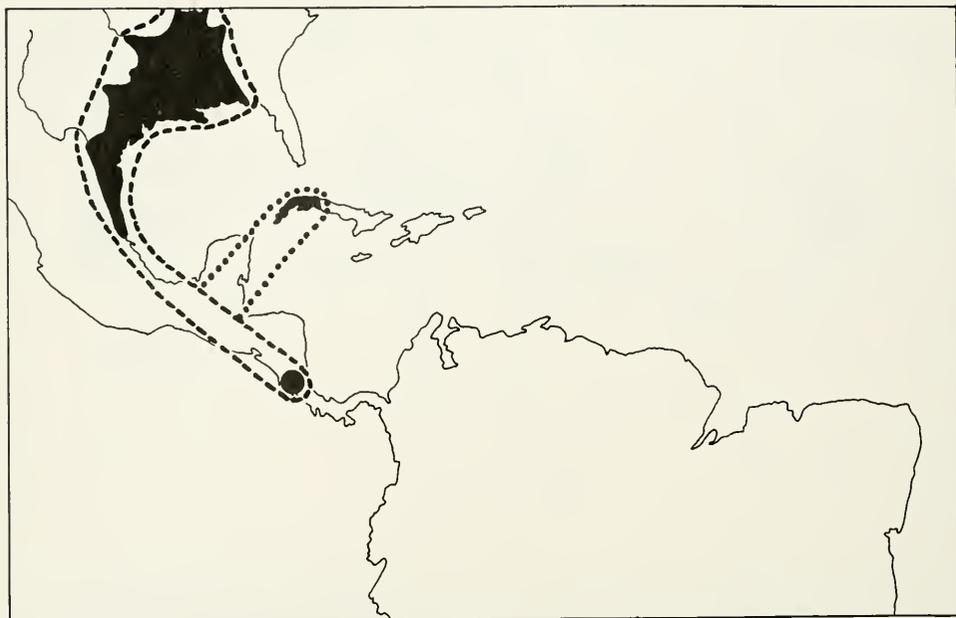


FIG. 72.—Track analysis of the *spatula-tristoechus* species pair. Dashes enclose the range of *A. spatula*, dots connect the range of *A. tristoechus* with *A. spatula*.

these generalized tracks involve species of the *A. spatula* species group—the North American-Caribbean generalized track and the Caribbean-West African generalized track.

The *A. spatula* species group forms a track (Fig. 71) composed of species from North America, nuclear Middle America, Africa, and the Caribbean. Within this track is another (Fig. 72) composed of the two disjunct populations of *A. spatula* and the Caribbean *A. tristoechus*. Rosen (1975) concluded that the Recent *Atractosteus* distributions in the Caribbean region were probably a part of an older North American-Caribbean generalized track of Pangean or Laurasian affinities, as opposed to a younger North American-Caribbean track with primarily Gondwanian affinities (a component of which would be *Gambusia*, for example). Additionally, Rosen concluded that the final determination of phylogenetic affinities among Recent *Atractosteus* would help determine the relative age of the vicariance event that produced *A. tristoechus*.

Within the *A. spatula* species group there are at least two levels of vicariance. First, the species group as a whole conforms to a track drawn between North America and Africa, and this track predates the formation of the Caribbean Region (to a time when, following Rosen's conclusions concerning the origin of the Caribbean, the region would still have been part of the Pacific seafloor). The minimum age of this track can be inferred from the current estimate of time of separation of western Africa from North America, which supposedly occurred during the Jurassic. Second, the *spatula-tristoechus* species pair conforms to the generalized North American-Caribbean track discussed by Rosen (1975), and is not necessarily older than similar distributions conforming to this track (i.e. *Gambusia*, etc.). Third, Rosen's conclusion that *Atractosteus* as a whole is Pangean is corroborated, since the most primitive species in the region, *A. tropicus*, has Pangean affinities and a relative age of vicariance older than the *A. spatula* group.

*Discussion.*—This brief statement of gar distributions can be summarized in a relative hierarchy of vicariance events: (1) The vicariance of the two genera probably occurred on Pangea and later dispersal events have obscured the original vicariance pattern. (2) The vicariance event that produced the *indicus-osseus* species pair is older than the event that produced the present distribution of the *L. oculatus* species group. (3) The *L. oculatus* species group is a component of a generalized Early Eocene track and thus has a minimum age of Early Eocene. (4) The distribution of the *A. spatula* species group was probably produced by a West Africa-North American vicariance event of Jurassic age, and this track is relatively older than the *spatula-tristoechus* track that is a component of a younger North American-Caribbean generalized track.

The model of gar biogeography presented above predicts that *Lepisosteus* gars will be found as a component of the African biota. Furthermore, the lack of gars from South America is interesting and it is possible that the vicariant sister group of gars may be found in the South American fossil biota.

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#### SUMMARY

(1) The objectives of this study were fourfold: to determine if the lepisosteids, or gars, are a monophyletic group, to determine which of the current theories of the relationships of gars to other actinopterygian groups is most highly

corroborated, to determine which nominal fossil and recent gar species could be recognized as valid species and what the interrelationships of these species are, and to describe the major features of gar biogeography.

(2) Hennig's (1966) phylogenetic method is used to study the first three objectives. Hennig's method is briefly summarized and several points taken up in detail. Croizat's (1958, 1962) biogeographic method is used for the biogeographic study.

(3) Anatomical features of gars are compared to those of other actinopterygian and teleostome groups. The analysis concentrates on the skull, visceral arches, pectoral girdle, and postcranial skeleton. At least twenty-seven characters are unique for gars among actinopterygian fishes and these characters corroborate a hypothesis of monophyly for gars as a group. Gars share seven derived (synapomorphic) characters with halecomorphs (*Amia*, etc.) and teleosts that they do not share with chondrosteans. These characters corroborate a monophyletic Neopterygii. *Amia* shares thirteen derived characters with teleosts that neither group share with gars, while *Amia* shares only two characters with gars not shared with teleosts that can not be refuted as derived, based on morphological criteria. Parsimony favors a monophyletic Halecostomi (*Amia* plus teleosts) rather than a monophyletic Holostei (*Amia* plus gars). It is also more parsimonious to consider the semionotids as halecostomes rather than as the sister group of gars, because the semionotid *Lepidotes* shares five derived characters with halecostomes while sharing only two loss characters with gars which can not be refuted as synapomorphies based on morphological criteria.

(4) The Division Ginglymodi, the family Lepisosteidae, and the two genera *Lepisosteus* and *Atractosteus* are diagnosed, and synonymies are provided. Each of the recognized species is diagnosed, described or redescribed, and

briefly compared to other species in its genus. Synonymies of Recent species include only name changes; the synonymies of fossil species include all literature citations found. Described fossil forms that cannot be diagnosed to species are placed at the level their preserved characters allow (i.e. *Lepisosteus* sp. indet., etc.). One species, *L. opertus*, is described as a new species from the Hell Creek Formation, Cretaceous, Montana. Other *Lepisosteus* gars recognized are: *L. cuneatus* (Eocene, North America); *L. platostomus* (Recent, North America); *L. indicus* (Cretaceous, India); *L. osseus* (Recent, North America); *L. fimbriatus* (Eocene to Oligocene, Europe); *L. oculatus* (Recent, North America), and *L. platyrhincus* (Recent, North America). Eight *Atractosteus* gars are recognized: *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* (Cuba and the Isle of Pines).

(5) Each genus is monophyletic based on derived characters.

(6) Within the genus *Lepisosteus*, *L. opertus* is the primitive sister species of all other *Lepisosteus* gars. *Lepisosteus cuneatus* is more primitive than *L. platostomus*. *Lepisosteus platostomus* is the sister species of a group composed of the *L. osseus-indicus* pair and the *L. oculatus* species group. Within the *L. oculatus* species group, *L. fimbriatus* is the sister species of the *oculatus-platyrhincus* species pair.

(7) Within *Atractosteus*, *A. strausi* is the primitive sister species of other *Atractosteus* gars. *Atractosteus tropicus* and *A. simplex* are relatively more primitive than the *A. spatula* species group. Within the *A. spatula* species group, *A. africanus* and *A. occidentalis* are *incertae sedis* while *A. atrox* is the sister species of the *spatula-tristoechus* species pair.

(8) A classification of Recent and fossil gars is presented.

(9) Track analysis of both *Lepisosteus* and *Atractosteus* indicate that both genera may have had Pangean distribution and thus may be as old as 180 million years before present. Within *Lepisosteus*, the track of the *osseus-indicus* species pair may be older than that of the *oculatus* species group. The *oculatus* species group track (Eastern North America to Europe) seems correlated with a generalized Eocene track based on mammalian distributions. Within

*Atractosteus* the *spatula* species group track connects North America and West Africa. This track may predate the formation of the Caribbean region. The track of the *spatula-tristoechus* species pair is correlated with a generalized North American-Caribbean track. The biogeographic model presented here predicts that *Lepisosteus* gars will be found in the fossil fauna of Africa and that the vicariant sister group of gars may be found among the fossil fauna of South America.

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APPENDIX A—MATERIAL EXAMINED

Specimens of gars used in this study are listed by Country or State and museum number for recent species, and Country, State (or region) and formation for fossil specimens. Fragmentary material not identifiable to species is not listed. The use of a "P." in front of the catalogue number indicates that the specimen is on deposit in the Paleontology Department of the institution cited (except the British Museum, Natural History), whereas no prefix in front of the number indicates that the specimen is on deposit in the Ichthyology Department of the institution cited. British Museum specimens are entirely from the Paleontology collections but may be labeled with or without the "P." Specimens catalogued in a separate osteological collection are prefixed by "ost." The following institutional abbreviations are used:

- AMNH, The American Museum of Natural History
- ANSP, Academy of Natural Sciences, Philadelphia
- BMNH, British Museum (Natural History)
- LACM, Los Angeles County Museum
- MCZ, Museum of Comparative Zoology, Harvard University
- MHNP, Muséum National d'Histoire Naturelle, Paris
- SMC, Sedgwick Museum, Cambridge University
- TU, Tulane University Collection of Fishes
- UMMP, University of Michigan Museum of Paleontology
- UMMZ, University of Michigan Museum of Zoology
- USNM, United States National Museum of Natural History

*Lepisosteus opertus*

Montana. Hell Creek Formation: MCZ P.13392 (holotype); MCZ P.13393-P.13397 (Paratypes); MCZ P.9374 (paratype). AMNH P.9323 (catalogued with specimens of *A. occidentalis*).

*Lepisosteus cuneatus*

Utah. Manti Formation: AMNH P.2517 (type). AMNH P.4622-P.4625; MCZ P.13325.

*Lepisosteus platostomus*

Arkansas: TU 447722 (2 spec.); TU 59709 (1 spec.). Kansas: ANSP 621 (1 spec., type *Cylindrosteus scabriceps* Cope). Illinois: UMMZ 14705 (4 spec.). Louisiana: TU ost. 297-299 (1 spec. each); TU ost.397-398 (1 spec. each); TU 47529 (3 spec.); TU 47546 (4 spec.); TU 47579 (2 spec.); TU 47657 (1 spec.); TU 70151 (2 spec.); TU 87357 (7 spec.); USNM 172825 (6 spec.); USNM 173088 (2 spec.). Iowa: UMMZ 10115 (9 spec.). Mississippi: USNM 129249 (6 spec.); USNM 129334 (2 spec.); USNM 129342 (8 spec.); USNM 129459 (5 spec.). Missouri: TU 53817 (8 spec.); UMMZ 147916 (2 spec.); UMMZ 190842 (1 spec.); UMMZ 190846 (2 spec.). Nebraska: UMMZ 134778 (1 spec.). Tennessee: USNM 32373 (1 spec.).

*Lepisosteus indicus*

India. Madhya Pradesh, Dongargoan, Lameta Beds: BMNH P.12178 (type); 40 mi. WNW of Nagpur; BMNH P.12186 near Takli; BMNH P.12185.

*Lepisosteus osseus*

Florida: LACM 33915-33921 (22 spec. total). Indiana: USNM 64917 (1 spec.). Iowa: UMMZ 173448 (3 spec.). Kentucky: USNM 89440 (1 spec.); UMMZ 174554 (4 spec.); UMMZ 174558 (3 spec.); UMMZ 180463 (1 spec.); UMMZ 182051 (1 spec.); UMMZ 189179 (4 spec.); UMMZ 56017 (100 spec.); UMMZ 60648 (4 spec.); UMMZ 82335 (1 spec.). Mississippi: USNM 129231 (1 spec.). Missouri: UMMZ 147917 (4 spec.); UMMZ 148093 (1 spec.); UMMZ 148825 (3 spec.); UMMZ 150213 (2 spec.); UMMZ 150762 (1 spec.). New York: AMNH 599 (1 spec.); AMNH 28657 (2 spec.); USNM 69947 (1 spec.). Ohio: ANSP 77987 (1 spec.). Texas: USNM 89430 (1 spec.); AMNH uncat. (4 spec.).

*Lepisosteus fimbriatus*

England, U.K. London. Dulvic, Woolwich Beds: BMNH P.5504; P.15488; P.33531; P.37201; P.39001; P.40338; P.41080. Hants., Barton Beds: BMNH P.12625; P.13057; P.39185-39189. Headon Beds: BMNH P.1529 and P.1529a; P.1700; P.13330; P.21058; 25252 and 25254 (types); 25258; P.27603; P.27607; P.27706; 28540; P.30295; P.33522-33526; P.33530; P.38104; P.46388-46389; P.47568-47569; SMC P.31389-31405; SMC P.31414. Kent, Oldhaven Beds: BMNH P.15280; P.16695-16696; P.31181. Blackheath Beds: BMNH P.14610; P.14613; P.14635-14637; P.14640;

P.14680; P.14753; P.16333-16334; P.19884; P.19908-19933; P.20010-20018; P.28066-28067; P.28575-28576; P.39313; P.1611a-i; P.46074-46075; P.51284; P.51297; P.51648; P.55510; P.55512-55517; P.55742-55748; P.55941-55947. Suffolk Pebble Beds: BMNH 29017. *Sussex*, Worthing: BMNH P.20127. Thornton Beds: P.38602. *France*. Paris Basin: MHNP P.8959; MHNP P.1874-638; MHNP P.4-1876; MHNP Lemoine collections, lots 1-3.

### *Lepisosteus oculatus*

*Alabama*: UMMZ 103506 (1 spec.). *Arkansas*: UMMZ 123149 (1 spec.). *Florida*: LACM 33914-33916 (22 spec. total); LACM 33912 (1 spec.); TU 23157 (1 spec.); TU 23795 (1 spec.); TU 23837 (1 spec.); TU 40572 (1 spec.); UMMZ 165168 (1 spec.). *Louisiana*: TU 268 (1 spec.); TU ost.300 (1 spec.); TU 6376 (1 spec.); TU 6506 (1 spec.); TU 11447 (5 spec.); TU 11618 (2 spec.); TU 13877 (3 spec.); TU 16842 (1 spec.); TU 17115 (2 spec.); TU 17680 (1 spec.); TU 41453 (1 spec.); UMMZ 170787 (1 spec.); USNM 172093 (1 spec.). *Michigan*: UMMZ 55062 (holotype); UMMZ 166511 (1 spec.); UMMZ 178806 (1 spec.). *Mississippi*: TU 85996 (3 spec.); TU 86199 (1 spec.); TU 86464 (1 spec.). *Texas*: TU 22289 (5 spec.); TU 24597 (2 spec.); TU 66629 (1 spec.); TU 85567 (1 spec.); UMMZ 165203 (2 spec.); UMMZ 165210 (1 spec.); UMMZ 166184 (1 spec.).

### *Lepisosteus platyrhincus*

*Florida*: LACM 33912-33913 (22 spec. total); UMMZ 158596 (1 spec.); UMMZ 158624 (7 spec.); UMMZ 159805 (5 spec.); UMMZ 166536 (1 spec.); USNM 26214 (1 spec.); USNM 92832 (1 spec.); USNM 133399 (1 spec.); USNM 133429 (4 spec.). *Georgia*: UMMZ 158093 (1 spec.).

### *Atractosteus trausi*

*Germany*. Vicinity of Darmstadt, Messel Locality: AMNH P.4626; AMNH 33839; AMNH 33856; also 16 uncatalogued casts of privately held specimens at AMNH; BMNH P.33506-33519.

### *Atractosteus tropicus*

*Costa Rica*: UMMZ 175920 (1 spec.); USNM 6806 (1 spec., holotype). *Guatemala*: AMNH 22092-22099 (1 spec. each); AMNH 25192 (3 spec.); AMNH 25622 (1 spec.);

AMNH 25649 (4 spec.); AMNH 25790 (1 spec.); AMNH 27937 (1 spec.); AMNH 28075-28076 (1 spec. each); AMNH 33851 (1 spec.); UMMZ 144241 (1 spec.); UMMZ 144244 (1 spec.); UMMZ 144247-144249 (1 spec. each); UMMZ 144251-144252 (1 spec. each); UMMZ 144254 (1 spec.). *Mexico*: TU 84923 (10 spec.); UMMZ 184612 (2 spec.); UMMZ 184631 (1 spec.); UMMZ 187727 (1 spec.); UMMZ 187747 (1 spec.); UMMZ 187793 (1 spec.). *Nicaragua*: TU 24277 (2 spec.); USNM 44175 (1 spec.); USNM 120715 (1 spec.).

### *Atractosteus simplex*

*Wyoming*. Bridger Formation: USNM P.2174 (type); USNM P.21173 (cotype). Green River Formation: AMNH P.4302; AMNH P.4305; MCZ P.5318; USNM P.22752. *New Mexico*. Wasatch Formation: USNM P.2582 (type of *C. aganus* Cope); USNM P.2584 (type of *C. interger* Cope).

### *Atractosteus occidentalis*

*Montana*. Hell Creek Formation: AMNH P.4304; BMNH P.56533-56537; MCZ P.9377-9379; MCZ P.9385. Lance Formation: BMNH P.48140-48153. Laramie Formation: BMNH P.10738-10739. *Canada*. Belly River Formation, Alberta: BMNH P.11906, BMNH P.12222-12223.

### *Atractosteus atrox*

*Wyoming*. Bridger Formation: USNM P.2145 (type); USNM P.4755; MCZ P.5168. Green River Formation: USNM P.3974 (type *Clastes anax* Cope).

### *Atractosteus spatula*

*Louisiana*: TU ost.119-123; TU ost.131; TU ost.315; TU ost.347-348; TU ost.351-353; TU ost.364-365 (1 spec. each); TU 17115 (2 spec.). *Texas*: UMMP 55462-55463; UMMZ 111049 (1 spec. each); UMMZ 1131001 (12 spec.); UMMZ 131165 (1 spec.). *Mexico*: TU ost.415 (parts of 5 spec.); TU ost.477 (parts of 8 spec.); USNM 1003 (1 spec., type *A. belanderi* Girard). *Nicaragua*: TU ost.388.

### *Atractosteus tristoechus*

*Cuba*: AMNH 3097 (9 spec.); UMMZ 30745 (1 spec.); USNM 12496 (1 spec., type *L. manjuari* Poy); USNM 24794 (1 spec.); USNM 11309 (parts of 5 spec.).



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