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THE PHYLOGENY AND BIOGEOGRAPHY OF FOSSIL AND RECENT GARS (ACTINOPTERYGII: LEPISOSTEIDAE)

by

E. O. Wiley, III

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York

1976

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January 28, 1976
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Abstract

The relationships of gars to other actinopterygian fishes, the number of recognizable species of gars, the relationships of these species, and the biogeography of these species were investigated. The phylogenetic method of Hennig (1966) was 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 was used to describe the major features of gar biogeography.

Gars were found to comprise a monophyletic group. Gars are the sister-group of the Halecostomi (Amiidae plus Teleostei). These three taxa comprise another monophyletic group, the Neopterygii. The Neopterygii is 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 an undescribed fossil species from the Cretaceous of Montana and the following seven species in approximate phylogenetic order: L. cuneatus (Eocene, North America); L. platostomus (Recent, North America); L. indicus (Cretaceous, India); L. osseus (Recent, North America); L. finbratus(Eocene and Oligocene, Europe);

L. oculatus (Recent, North America); *L. platyrhincus* (Recent, North America). The interrelationships of these species are discussed.

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

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

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To my colleagues and friends at the American Museum of Natural History I express my thanks for many hours of discussion about gars and systematic theory. Special thanks go to Dr. Donn E. Rosen whose help and encouragement throughout the project are gratefully acknowledged. Thanks also to Dr. Gareth Nelson who spent many hours discussing problems of fish phylogeny and systematics with me and who taught me many techniques used during the project. Dr. Bobb Schaeffer gave me valuable advice and guidance on the fossils. Mr. Walter Sorensen helped and guided me in fossil preparation. The section concerning ancestor recognition grew out of a dialogue with my colleague George Englemann; we expect to publish our thoughts on this subject in an expanded joint paper. Ms. Louise LoPresti typed the rough draft, Ms. Lynne Judge and Ms. Joan Mey typed the final draft. Their skills are appreciated.

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Introduction

The lepisosteids, or gars, are carnivorous fishes of sluggish habits that 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 (Eocene). 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 occurence in these habitats). Anatomically, they combine various primitive (plesiomorphous) and derived (apomorphous) characters. Notably primitive characters include interlocking ganoid scales, skull roofing bones with enameloid tubercles, a semi-heterocercal tail, and fulcral scales on the medial fins (Suttkus, 1963; Patterson, 1973). Derived characters not found in any other group of actinopterygians include an attenuated snout produced by ethmoid elongation, opisthocoelous vertebrae and plicidentine teeth.

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

Early development: Wright, 1879; Balfour and Parker, 1882 (many aspects of both development and structure, comparisons with other fishes); Beard, 1889; Mark, 1890; Dean, 1895a and b, 1896 a and b (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 (corpusles of Stannius); Kullin, 1950 (forebrain); Bodemer, 1957 (extrinsic ocular muscles); Kerr, 1967 (teeth); Jessen, 1972 (pectoral girdle).

Skull structure: Veit, loc. cit.; Baur, 1889a (comparison of occipital region with Amia); Allis, 1919 (comparison of otic region with other fishes); De Beer, 1926 (comparison of orbito-temporal region with other fishes); Rayner, 1948 (neurocranial ossifications compared to other fishes); Patterson, 1973 (comparisons with other neopterygians), 1975 (comparison with other actinopterygians); Reagan, 1923 (skeleton, with comparisons); Mayhew, 1924 (skull ossifications); Gregory, 1933 (comparisons with other fishes); Holmgreen and Stensio, 1936 (skull and visceral arches); Westoll, 1937 (cheek bones), Stensio, 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; Stensio, 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 Stensio, 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, 1967.

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

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

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

Other anatomical studies include: Wyman, 1844 (tooth structure); Müller, 1844, (gut); Wilder, 1877 (brain), 1878, (gut); Hyrtil, 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) provides 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 are usually put in an order or division of their own (Ginglymodi of Cope, 1872; Patterson, 1973; Lepidosteiformes of Berg, 1940, Lepidostei 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 chondrostean, 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 have since been placed in synonomy. The proliferation of synonyms was brought about primarily by a lack of understanding 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 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 of these efforts to comprehend gar relationships resulted in a complicated nomenclature which has since been simplified by the 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, redescribed 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 long-snouted morphotype from the coastal plain of Texas. The status of this morphotype can not 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 four species are 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 recognized 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 their 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 synonomies provided. The synonomies of Recent species include only name changes or significant systematic references whereas that of fossil forms includes 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 this section 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 intraspecific variation which might cause problems in identification of those taxa.

In the analysis of the phylogenetic relationships among gars, each character is analyzed to determine its relative apomorphous (derived) or plesiomorphous (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 (in press) has discussed the distribution of Atractosteus in relation to generalized features of the Middle American and Antillian biotas. Rosen's discussion followed a "vicariance" methodology proposed by Croziat (1958, 1962) and summarized by Croziat, 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 and locality (and formation, if a fossil) below. Other actinopterygian specimens are referred to by catalogue number in either the text or figures. Institutional and structural abbreviations are found in the abbreviation section.

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 *Atractosteus strausi* specimens 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. Both Bausch and Lomb and Wild dissecting microscopes were used. Meristic counts follow those of Suttkus (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 enameloid 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 melanophores 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 meristics presented here are meant to represent statistical samples, nor to characterize adequately the variation expected in Recent North American species. Dr. Royal Suttkus has taken and continues to take extensive meristic and morphometric data on Recent North American 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 measurements reported as 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: (1) if the Recent species is not well known (A. tristoechus, A. tropicus);or (2) if less than 10 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 the enameloid development of the premaxillary process to the posterior junction of the parietals.

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

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

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

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

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

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

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

PmL (Length of premaxillary process): distance from the posterior junction of the processes to the anterior end of the surface ornamentation.

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

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

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

OpW (Opercular width): from the posterior junction of the opercular and subopercular anterior to the end of the 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, b). Popper's approach dictates the 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 the valid tests applied to them. Where conflicting hypotheses compete because none are totally falsified by the evidence at hand, the hypothesis which 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 scientific.

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,b, 1973a, 1974; Crawson, 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, 1972a, 1972b, 1974; Sneath and Sokal, 1973;

Sokal, 1975, and others). I do not intend to discuss all the pros and cons of the arguments presented by the above mentioned authors. I will state that where criticisms of the phylogenetic method have proven valid that part of the methodology has been de-emphasized or dropped without invalidating the methodology (for example, the "deviation rule," Schlee, 1971 and the "biogeographic" or "progression" rule, Croziat et.al., 1974, and Nelson, 1974). Other objections have either proved insubstantial or have been successfully answered by the proponents of the methodology (for example, Mayr's 1974 objections are answered by Rosen, 1974b, and Hennig, 1975). There are two alternate 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 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 briefly summarized. 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 valid grouping criteria. Taxa which share a 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 which indicate immediate common ancestry are used to elucidate relationships between sister groups. Characters which purport to demonstrate sister-group relationships are termed apomorphous characters and taxa which share these characters are said to have synapomorphous characters in common. Characters which indicate a phylogenetic relationship but not a sister-group relationship are termed plesiomorphic characters. Characters which 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 apomorphous, 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 controversy of ancestor recognition versus hypothetical ancestors is discussed.

Homology. A concept of homology is basic to any methodology which makes comparisons between two or more organsism or taxa. In a general sense, characters which 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 types 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 definition like that discussed by Sneath and Sokal (1973) Those interested in phylogenetic relationships will adopt a definition similar to that of Simpson (1961), Bock, (1969), or Hennig (1966). I have argued that a phylogenetic definition is preferable to a phenetic definition because it leads to hypotheses of homology which contains all the potential falsifiying 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 which display the character (Wiley, 1975, modified from Hennig, 1966). There are two logical derivations of this definition. First, characters which are derived in the immediate common ancestor of the taxa compared, and retained in these taxa may be termed synapomorphous characters. Such characters are hypothesized as having originated in the immediate ancestral species as unique or autapomorphous characters. The presence of these characters in the descendent taxa is evidence of immediate common ancestry of the descendent taxa. Second, characters which 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. 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 non-homologous 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 hypothesis 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 branching sequences it incorporates. For example, a hypothesis incorporating four species exists on a higher level of universality than a hypothesis incorporating three species.

At any particular level of phylogenetic universality other than the highest both plesiomorphous and apomorphous characters must be considered because the investigator must sort out those characters present in the organisms which demonstrate immediate common ancestry from those which do not. The principle may be framed as a question: Which characters are uniquely derived in ancestors included in the hypothesis and which are uniquely derived in ancestors not included in the hypothesis, but retained by ancestors included in the hypothesis? The synapomorphies of a phylogenetic hypothesis are the characters which demonstrate immediate common ancestry at the level of universality considered, whereas symplesiomorphies demonstrate immediate common ancestry at a level of universality higher than that under consideration. Thus, symplesiomorphies are not relevant to the problem at hand (as well as being untestable hypotheses for reasons discussed above). It is characteristic of symplesiomorphies that their nature changes relative to the level of universality of the problem. Plesiomorphies become apomorphies when the level of universality is raised high enough. It is characteristic of synapomorphies that they do not change relative to the level of universality of the problem so long as the original branching sequence is retained in the hypothesis. They become symplesiomorphies only when a subset of the problem is being considered, i.e. when branches which form a subset of one of the original branches are investigated. Plesiomorphies, therefore display three characteristics: (1) they cannot elucidate problems of immediate common ancestry; (2) they are non-testable hypotheses of homology; and (3) their nature is changed by raising the level of universality of the phylogenetic hypotheses.

Autapomorphous characters properly belong only to species. When the term is applied to a character belonging to a higher taxon, it is only because that higher taxon is considered a single entity for the purpose of testing a 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 (1) it cannot elucidate problems of immediate ancestry between taxa, and (2) it is an untestable homology (because the ancestor is not observed). Two further characteristics are apparent: (1) that its nature does not change as the level of universality is raised (like a synapomorphy), and (2) 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 rather 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 which 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 a 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 other hypotheses of synapomorphy are shown to be symplesiomorphies, or (2) non-homologies. Neither of these conditions represents a valid test and therefore neither would represent valid refutations of the phylogenetic hypothesis. If the 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 (1) by finding the character in the sister group of the entire system tested, (2) by finding the character so commonly outside the group that it is considered a symplesiomorphy, or (3) by applying a developmental or ontogenic rule of character transformation. (3) automatically raises the level of phylogenetic inquiry because 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 distribution of characters among the three taxa provide deductive tests of the relationship. Without reference to Hennig's specific method but with reference to any test of relationship we may say that the only tests which can be considered valid attempts to refute a given three taxon problem are those which involve 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 to only one are congruent with the three 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 the most parsimonious. Hennig's (1966) method differs fundamentally from a purely phenetic method in that all of the shared characters are not used to refute a given relationship. Rather, only synapomorphous characters are used. Such testing can be accomplished only in an open system, that is, by considering taxa outside the three taxon system. Such considerations may be termed out-group comparisons. The one condition placed on this procedure is that the three taxa must form a monophyletic group. The designation of out-groups 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 out-group 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 a 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 investigator will have to reject certain characters as valid indicators of relationship. And, it is the characters analyzed as symplesiomorphies or nonhomologies which can objectively be rejected as valid indicators of relationship within the three taxon problem. This is because (1) they are not pertinent to the elucidation of immediate common ancestry and represent *ad hoc* hypotheses, as discussed above, and (2) 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 and 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 valid 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.

Hypothetical vs. Recognized Ancestors. A major portion of this study is concerned with testing relationships between fossil and Recent gars. One of the basic questions to be settled in such an analysis is whether hypotheses of ancestor-descendent relationships are to be permitted in the analysis, that is, whether ancestral species can be recognized. Nelson (1973a) outlined two concepts of kinship in phylogeny reconstruction: (1) either ancestral units are assumed to be know or potentially knowable empirically; or (2) ancestral units are assumed to be empirically unknowable. Patterson and Rosen (in press) have argued that this ancestral unit must be a species or population and that higher taxa cannot be considered ancestral units. This argument is based primarily on a strict concept of monophyly sensu Hennig (1966). This concept leads to the conclusion that a higher taxon cannot be considered ancestral because, if it were, it would not be monophyletic. This is because some of its included members would be more closely related to taxa outside of its group than to some taxa inside its group. 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 (1972a, 1972b), 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. Since higher taxa do not evolve, then they cannot be considered ancestral units. The reality of higher taxa is based solely upon whether or not 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 descendents of an ancestor be placed in the same group as the ancestor. This definition conforms to basic set theory and is methodologically precise. The removal of a species or group of species from a taxon which includes its ancestor and sister group and then terming this taxon monophyletic and ancestral to the species or group of species is untenable because: (1) it breaks up a logical set of two logical subsets into one logical set (the species or group of species) and one illogical set (the "ancestral" taxon whose general components can no longer be logically defined), and (2) it makes the term monophyly an open term, that is, any taxon could be termed monophyletic (Hennig, 1966). Third, Rosen (in press) has pointed out that the use of non-monophyletic groups sensu Hennig (1966) in biogeographic analysis leads to distribution patterns which are incomplete 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 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.

Patterson and Rosen (in press) have dealt with the problem of ancestor recognition. They conclude that:

(1) The objections of Hennig (1966), Crowson (1970), and others to the integration of fossil and Recent taxa into a single analysis can be circumvented by regarding fossil taxa as terminal branches.

(2) An ancestral unit, if recognized, must be a species or lower group.

(3) The identification of a particular fossil species as an ancestor of a particular group must be preceded by an analysis which demonstrates that the particular fossil species is a member of the group to which it is supposedly ancestral. In other words, by demonstrating that the pattern of characters of the fossil species does not refute

an hypothesis that the fossil species belongs to the group. And, this analysis is a cladistic analysis, based on cladistic information.

(4) Although the fossil species must share all the group membership characters of the group (the synapomorphies of the group), it cannot share a synapomorphy with any one or other member of the group. That is, its relationship to the group must be equal to its relationship with all members of the group, it can not be more closely related to one member of the group than to another.

(5) This type of analysis becomes cladistic only by assuming an evolutionary process which assumes an ancestral-descendant interpretation of the taxa and their observed characters.

(6) The identification of ancestral species in the fossil record is tautological because:

(characters of ancestry) = (characters of group membership)

but: (characters of ancestry) - (characters of group membership)

=0 thus: (characters of ancestry) = (characters assumed ancestral), tautology.

If one wishes to ignore the tautology, or if one concludes that the reasoning which led to the tautology is invalid, then the problem becomes a question of whether ancestor-descendent hypotheses are testable as scientific hypotheses sensu Popper (1968), as Bock (1973) has stated, or whether they are nontestable. This question is important methodologically for two reasons, First, if these hypotheses are scientific in the sense that they are objectively testable, then they would seem to convey more information than the sister group statements. Second, if they are objectively testable then excluding them from Hennig's methodology seems non-objective and the axion of excluding ancestor-descendent hypotheses from phylogenetic analysis would seem invalid.

In the abstract, three conditions must be met for a fossil species to be considered ancestral to other species or higher taxa on purely morphological grounds (without reference to age of occurrence). First, in all characters where the supposed ancestor differs from descendents it must have the relatively plesiomorphous character in the transformation series. Second, it must have all of the apomorphous characters shared by the descendent taxa and these characters must have existed as autapomorphies in the ancestral species before the speciation event which resulted in the descendent species. Third, it must have no additional apomorphies of its own, that is, it cannot have any autopomorphies which were not passed on to its descendent taxa.

It would seem that the strongest case for testing ancestor-descendent relationships by the holomorpholocical method is that every plesiomorphy found in the supposed ancestor represents a corroboration of the hypothesis whereas finding an autapomorphy would result in a refutation of the hypothesis. But, plesiomorphies are untestable ad hoc hypotheses of homology and thus they can not be used to test relationships at the level of universality they existed as plesiomorphies. Thus, their application to an ancestor-descendent hypothesis does not represent valid tests of the hypothesis and corroboration of an ancestor-descendent hypothesis is not possible. If autapomorphies did represent valid tests then we would have a paradox, a hypothesis which could be refuted but which had no valid corroborating instances. But as recognized by Hennig (1966) and others, unique characters do not indicate relationships, they define taxa. And, simply because a character is unique does not automatically dictate that it is autapomorphic, (the gar snout sensory canal pattern is unique but not autapomorphic, see discussion below). The effect of accepting a unique character as autapomorphic is the effect of rejecting the alternate character as apomorphous and accepting it on the grounds of parsimony as autapomorphous. I would therefore suggest that autapomorphies are ad hoc hypotheses resulting in an appeal to parsimony, and thus could not be used to test hypotheses of ancestral-descendent relationships.

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, Croziat (1958, 1962), and summarized by Croziat, Nelson, and Rosen (1974) and Rosen (1974a).

The vicariance method attempts to find general patterns of distribution so that a general solution can be sought which would 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, distributional patterns comprising more than a single track. These 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 should have originated by the separate change 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 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 which would affect the biota as a whole to produce the observed pattern rather than separate explanations which would affect 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.

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 are 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 whereas no prefix in front of the number indicates that the specimen is on deposit in the Ichthyology Department of the institution cited. 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, Tuland 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 (catalogue numbers for this new species are on request).

Lepisosteus cuneatus

Utah. Manti Formation: AMNH P.2517 (type). AMNH P.4622-4625; 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. 297-290 (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: Dongargoan, Central Provinces: 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.). Michigan: UMMZ 173340 (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. Dulwick, Woolwich Beds: BMNH P.5504; P.15588; P.20127; P. 33531; P.37201; P.38602; P.39001; P.40338; P.41080. Hants., Barton Beds: BMNH P.12625; P.13057; P.39185-39189. Headron Beds: BMNH P.1529 and 1529a; P.1700; P.13330; P.21058; P.25252 and P.25254 (types); P.25258; P.27603; P.27607; P.27706; P.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.16695-16696; P.31189. Blackheath Beds: BMNH P.14610; P.14613; P.14635-14637; P.14640; P.14680; P.14753; P.15280; P.16333-16334; P.19884; P.19908-19933; P.20010-20018; P.28066-28067; P.28575-28576; P.39313;

P.41611a-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 P.29017. 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 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 strausi

Germany. Vicinity of Darmstadt, Messel Formation: 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 2209-22099 (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 C. interger Cope).

Atractosteus occidentalis

Wyoming. 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.351-352; TU ost.364-365 (1 spec. each); TU 17115 (2 spec.). Texas: UMMP 55462-55463; UMMZ 111049 (1 spec.); 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 Garard). Nicaragua: TU ost.388.

Atractosteus tristoechus

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

Abbreviations Used in Figures

a, angular

ACH, anterior ceratohyal

abd hyo, abductor hyoides

Ant, antorbital

Ar, articular

Arto, articular surface of bone named

B, branchiostegal

BB 1-4, basibranchials 1-4

BBC, basibranchial capula

BHTP, basihyal tooth plates

BOC, basioccipital

c, coronoid

Clm, cleithrum

CO, circumorbital

comm, commissure

d, dentary

Dpt, dermopterotic

Dsp, dermosphenotic

E, ethmoid

EB 1-4, epibranchials 1-4

Ecpt, ectopterygoid

Enpt, Endopterygoid

Exo, exoccipital

FR, frontal

HA, hyoid arch

HB 1-4, hypobranchial 1-4

HH, hypohyal

Hyo, hyomandibular

IB, 1-3, infrapharyngobranchials 1-3

I. com, internerial commissure

IO, infraorbital

Ioc, infraorbital canal

La, lacrimel

LABE, levator arcus branchialis, exterior

LABEI, levator arcus branchialis, interior

lwp, lateral wing of prearticular

Mc

MEC, Meckel's cartilage

Mpt, metapterygoid

msc, mandibular sensory canal

MTP, medial toothplates

M.W. clm., medial wing of cleithrum

Na, nasal

OD, oblique dorsalis

Ors, orbitosphenoid

Op, opercular

OV, oblique ventralis

tend. OVp, tendon of posterior oblique ventralis p, prearticular

Pa, parietal

PCH, posterior ceratohyal

P com., post-nares commissure

Pmx, premaxillary

Pop, preopercular

pr , process

Pro., prootic

pro hyo, protractor hyoides

Psp, parasphenoid

Pt, post-temporal

Pto, pterotic

Pts,

Q, quadrate

Qj, quadratojugal

r, retroarticular

RAB, retractor arcus branchialis

RC, rectus communis

Ro, rostral

Ro-Deth, rosto-dermethmoid

s, surangular

SB, suprapharyngobranchial

Sclm, supracleithrum

Spo, sphenotic

So, suborbitals

Soc, supraoccipital

Sor, supraorbital sensory canal

St, supratemporal

Sthyo, sternohyoides

Sym, symplectic

Sop, subopercular

TD, transverse dorsalis

tend, tendon

UP, uncinate process

Vo, vomer

The Relationship of Gars to Other Actinopterygians

Gars have traditionally been considered primitive actinopterygian fishes but their exact sister group relationships have been subject to dispute. Müller (1844) included the gars with the polypterids in his order Holostei. Huxley (1861) added Amia to the Holostei and removed polypterids to 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, 1930). 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 an effort to assess the relationships of gars to other actinopterygians, I have attempted below to establish which of the characteristics displayed by gars are autapomorphic, which are synapomorphic with one or more non-gar actinopterygian groups, and which are symplesiomorphic or non homologous 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 (halacostomes) than are chondrosteans (Patterson, 1973, fig. 11c).

(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).

The Skull

The pattern of dermal and endochondral ossifications is basically similar in gars, other neopterygians, and in many chonodrosteans, making hypotheses of homology possible (Patterson, 1973, p. 239). The pattern of dermal ossification of gars is illustrated in Figure 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, p. 499) reviewed the occurrence of ethmoid ossifications in various actinopterygian groups and concluded that ethmoid ossifications are primitive for osteichthyans. Lateral ethmoids are found in teleosts, *Amia*, large *Acipenser*, *Polypterus*, and *Latimeria* (Patterson, 1975). They are also found in palaeoniscoids (*Bergeria*, Neilsen, 1949; *Perleidus*, Patterson, 1975), fossil halecomorphs (*Caturus*, Rayner, 1948; *Sinamia*, Stensio, 1935), "holosteans" (*Macrepistius*, Schaeffer, 1971; *Lepidotes*, Patterson, 1975). Fully ossified forms such as some palaeoniscoids, all parasemionotids, and the semionotiforms *Heterolepidotes* and *Dapedium*, probably had internal ossified ethmoids during development (Patterson, 1975, p. 499). I conclude that the elongation of the ethmoid cartilage and the lack of ossifications in this cartilage are synapomorphous characters shared by gars.

Gars and palaeoniscoids lack an endoskeletal rostrum of the type seen in Recent chondrosteans, saurichthyids, amiids, and teleosts. Independent ossifications 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, p. 502). Patterson (1975) concludes 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 a 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 preethmoids of Amia and Pachycormus, the supra- 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 which carry the infraorbital sensory canal.

Gars differ from other actinopterygians in having two commissures between the supra- 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 which runs from the antorbital to the premaxillary arm posterior to the nares (Jollie, 1969). Jollie (1969) states 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 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 which traverses 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 where the infra- 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 Watson, 1937). Among sarcopterygians there are several snout patterns. The dipnoans Protopterus (Panchen,1967) and Neoceratodus (Stensio, 1947) have no commissures between the supra- 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 supra- and infraorbital canals in front of the snout and the infraorbital canals are connected to each other across the snout (Holoptychius, Jarvick, 1947; Eusthenopteron, Jarvick, 1944; see Stensio, 1947, for summary but note that figure 29b, p. 106 is probably incorrect). In Latimeria chalumnae there are commissures between the supra- 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. It is interesting to note here that *Polypterus* displays the sarcopterygian pattern (see Jollie, 1969, and Stensio, 1947, for illustrations).

Within the Actinopterygii the primitive condition (fig. 3c) seems to be that where 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* (Neilsen, 1942), *Bergeria* and *Australosomus* (Neilsen, 1949), *Moythomasia* (Jessen, 1968),*Ategotrachelus*, *Kentuckia* and others (Gardiner, 1963)but not in *Canobius* and *Babastrania*). This snout sensory canal pattern is probably apomorphic for the Actinopterygii and thus plesiomorphic within the group. What the plesiomorphous pattern is for teleostomes in general is not clear. The pattern seen in the coelacanth *Latermeria* incorporates both the rhipidistian and actinopterygian patterns. Dipnoans have a different, and presumable apomorphous, pattern. But whatever the basic teleostome pattern may be it is logical to assume that the internarial commissure between the supra- 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 apomorphous 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 commissure of gars and teleosts? Jollie (1969) states that the internarial commissure of Amia calva is not fully developed until relatively late in development (200 mm). Allis (1889) figures 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 a infraorbital branch on the antorbital is apomorphous for neopterygians. Gars are unique in having both the plesiomorphous and apomorphous commissures. Amia and teleosts lack the internarial commissure of gars and and chondrosteans, an apomorphous condition. Further, Amia calva is autapomorphous in having the postnarial commissure between the nares.

The premaxilla of the gars includes a toothed anterior part, the premaxilla proper, and the premaxillary or nasal process (pmx, fig. 2, and Patterson, 1973) makes up as much as 50% of the length of the snout and carries the supraorbital 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 ethmo-nasals, 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., p. 510). Patterson also found that the lateral dermethmoids of philodophorids occupies 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 termed by Bjerring (1972) the rhinal bone. In contrast the gar premaxilla has either a single ossification center

(Aumonier, 1941, p. 20), or is derived from an anasmatic bone and parts of a sensory bone (Hammarburg, 1937). It would seem that the developmental sequence of the premaxilla of Amia and gars differs. 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 actionpterygians (see Patterson, 1973). Lepidotes has a single vomer (Rayner, 1948), a character which 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 autapomorphic. 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 consists of 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 an supratemporal series which 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 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 Neilsen, 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 palaenoscoids do not have a complete circumorbital ring. Rather, the nasals form the anterior borders of the orbits (*Pteronisculus*, *Boreosomus*, *Canobius*, and platysomids, Stensio, 1947; *Polypterus*, Jarvick, 1947). Others have a complete circumorbital series (*Cheirolepis*, Watson, 1925; *Dicellopyge*, 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 come 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 supra- and infraorbital canals relative to the dermal roofing bones show much variation within the Actinopterygii. In palaeoniscoids 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 dermopterotic (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 the presence of such commissures has apparently 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 (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, p. 245) interprets 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 which purports to demonstrate relationships is one found in the common ancestor of the taxa related. But the bulk of evidence leads to the conclusion that the common ancestor of amiids and teleosts had suborbitals and that primitive teleosts (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 suborbial mosaic of gars is a bone identified by Jollie (1962) as the dermohyal (Dhy, fig. 2). Patterson (1973, p. 245) concludes that the evidence for identification of this bone is weak, and that while it may be the dermohyal it could also be the homologue of the suprapreperculum. I agree with Patterson's conclusion 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 synopomorphy 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. Halecomorphs, 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) depends 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, a endochondral bone found in Amia, teleosts (Patterson, 1975), "Gogo palaeoniscids" (Gardiner, 1973), Pteronisculus (Neilson, 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 in unique in several respects (fig. 6). The quadrate is supported entirely by the ectopterygoid medially and the quadratojugal posteriorly. The quadrate is situated in 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 sympletic 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 ectoterygoid 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 Stensio (1936) agree with Patterson (1973) in identifying 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 is considered by Goodrich (1930) to be the plesiomorphous gnathostome condition. Schaeffer (1967b) and Gardiner (1973) disagree and state 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 (palaeoniscoids, 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 (as so far as a hyomandibular can be identified) and Recent sharks the ramus hyomandibularis VII passes the hyomandibula laterally and then branches. In rhipidistrian sarcopterygians (*Eustenopteron*, *Megalichthyes*, and other osteolepiforms and porolepiforms where the condition is known; Jarvik, 1954) and in coelacanths (*Nesides*, Jarvik, 1954; *Latimeria*, Millot and Anthony, 1958, 1965) the orientation of the ramus hyomandibularis VII to the hyomandibula 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 hyomandibula 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 studied by Nelson (1973b). He considered the presence of discrete articular, retroarticular, and mentomeckelian endochondral ossification 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 figure 7. Nelson

(1973b)states 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 mentions the bone in large sturgeons. It is also present in Pteronisculus (Neilsen, 1942), Latimeria, and 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 Meckels 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 Meckels 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 DeBeer (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 has been published by Patterson (1975). He summarized pertinent data from previous studies and added new information on the structure of the neurocranium of phylogenetically important taxa. The ossifications of the neurocranium of Lepisosteus occulatus are shown in figure 8.

Patterson (1975, p. 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 philodophorids. 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 Lepitodes 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. Further, the amiids have lost the pterotic (following Patterson, 1975). The loss of both the opisthotic and endochondral intercalar is, therefore, not a unique feature of only gars and Lepidotes within the Actinopterygii. Rather, 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 paleonisooids, 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 non-homologous.

Finally, gars have no anterior myodomes. The anterior myodomes are found in a number of chondrosteans, parasemionotids, Dapedium, caturids, and amiids (Patterson, 1975, pp. 515-516). Patterson considered the gar condition secondary; it would thus be a synapomorphous character of gars. Gars share with Polypterus and most primitive palaeoniscoids a transverse canal in the otic region, a characteristic Patterson (1973, p. 254) thought precludes 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, pp. 253-254) stated that the basipterygoid process of gars is intermediate between the condition in chondrosteans where the process is entirely endochondral (i.e. via the protic) and the derived condition in amiids and 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 basihyal tooth plates and branchiostegals (fig. 9). Gars, like amiids and chondrosteans, lack the basihyal of teleosts (Wijhe, 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 via connective tissue to the basihyal toothplates of the spatulate "tongue." The antérior 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 posterior ceratohyal and one articulates with the anterior ceratohyal, or occasionally at the junction of the two ceratohyals. That the most posterior ceratohyal is the homologue of the interopercular of halecostomes (DeBeer, 1937) has been rejected by McAllister (1968).

What, if any, phylogenetic significance can be attached to the low 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 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 originates 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 found 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 which 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 keeping 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 copula 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) considers plesiomorphic for the Actinopterygii. Gardiner (1973) states 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 palaeoniscids (Birgeria Stensio, 1921) and Pteronisculus (Neilsen, 1942). Gardiner (1973) reviewed the number of copula in other teleostomes. Four copulae, then, seem to be synapomorphous for the Neopterygii.

The position of the articulation of the hypobranchials to the basibranchial copulae also varies between actinopterygian groups. In gars (fig. 11a) hypobranchial I articulates at the junction of the basibranchials I and II hypobranchial II articulates at the junction of basibranchials II and III, hypobranchials III and IV and ceratobranchial V articulate with basibranchial III, and basibranchial IV supports no paired arch elements (Nelson, 1969a). In Pteronisculus, basibranchial I supports no paired arch elements and was termed the basihyal by Neilsen (1942).

Polyodon and *Amia* (figs. 11d, b) are similar to each other in having hypobranchials I and II articulating with basibranchial I. In *Polyodon*, hypobranchials I to III all articulate with basibranchial I and if this basibranchial is homologous to basibranchials I and II 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 hypobranchial IV penetrated by the ventral aorta. Gars have hypobranchials which are not penetrated by the ventral aorta, a condition hypothesized here as apomorphous.

Amia and gars have a perichondral ossification on the copulae between arches II and III (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 II in *Amia* and basibranchial III in gars, (2) perichondral ossifications of basibranchials are found in palaeoniscoids (Stensio, 1921; Neilsen, 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 an 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 apomorphous 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 uncinate processes (UP, fig. 12b). Chondrosteans lack uncinate processes (fig. 12a) whereas Amia and teleosts have uncinate processes on the third epibranchial as well as on the first two epibranchials (fig. 12c). In Amia the third uncinate process is not prominent and is cartilaginous whereas in teleosts it is well developed and ossified. I hypothesize that the lack of uncinate processes, the condition of chondrosteans, is plesiomorphous for actinopterygians. Gars, Amia, and teleosts share the synapomorphy of having uncinate processes. Gars have the relatively plesiomorphous condition of two uncinate processes relative to the three possessed by halecostomes.

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 is based on the observation that elasmobranchs and acanthodians have a fourth infrapharyngobranchial. Patterson's (1973) conjecture is based on the observation that all actinopterygians except teleosts lack a fourth infrapharyngobranchial. Acceptance of Nelson's (1969a) hypothesis would required 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 not homologous with the fourth infrapharyngobranchial of elasmobranchs and acanthodians.

Chondrosteans have infrapharyngobranchilas which are posteriorly supported by the epibranchials (fig. 12a; Gardiner, 1973; Neilsen, 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 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: (1) it is absent in other actinopterygian groups and (2) additional balls of cartilage are found in higher teleosts (Rosen, pers. comm.) and 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 endodermal visceral skeleton may be conveniently divided 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. Latimeria has retained the primitive osteichthyan features (Nelson, 1969a). Among chondrosteans, Pteroniscculus has several rows of toothplates associated with each arch (Neilsen, 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 I, II, and III, ceratobranchials II, III, and IV, and on epibranchial I. Gars have lost medial toothplates on ceratobranchial I. Two rows of medial toothplates (the plesiomorphous condition) are found on hypobranchials IV and infrapharyngobranchial II while several rows of toothplates are found on ceratobranchial V and infrapharyngobranchial III. 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 dentation. 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 III, IV, and possible V are involved). This conjecture 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 III 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 where 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 connecting the epibranchials with 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 transverse dorsalis and oblique dorsalis (fig. 13). I conclude that the 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. Tèleost 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 synapomorphous. 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 (1) the retractors of both gars and Amia originate on the vertebral column and insert on the third infrapharyngobranchial and (2) they have a similar embryological development, at least to the point that both are derived from the same muscles. 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 antero-lateral 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. The teleost Albula (fig. 13c) has 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 shows fibers with the transverse ventralis. I hypothesize that the presence of a transverse ventralis is an synapomorphy of neopterygians, that the 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 esophagal cavities. In the chondostreans Polyodon and Acipenser, there are two muscles, the transverse ventralis running between the fifth ceratobranchials and the coroco-branchial which originate on the midline connective tissue and insert on the corocoid of the pectoral girdle. In Polyodon the coracoid-branchial 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 coracoid-branchialis and it is undifferentiated from the circular muscle layer of the esophagus. In *Acipenser* the coracoid-branchialis is better defined, originating at the midline as a pair of discrete muscles connected via 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 coracoid-branchialis does not originate on the midline connective tissue but on the lateral surfaces of the fifth ceratobranchials. In *Amia* and gars the coracoid branchialis 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.

Post Cranial Skeleton

Dermal components of the pectoral girdle. The dermal pectoral girdle of gars includes the post-temporal, supracleithrum, and cleithrum (fig. 15). The post-temporal articulates with the supratemporals 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 supracleithrum via the concave supracleithral 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, a structure which articulates with the dermo-intercalar (see figures in Jessen, 1972; pers. observ. of Elops, Megalops, Albula, Clupea, Osteoglossum, and Salmo). Patterson (pers. comm.) reported the process in at least some semionotids. The presence of a post-temporal process in halecostomes is hypothesized apomorphous relative to its absence in gars and chondrosteans. The mode of articulation between the post-temporal and supracleithrum in gars is unique and hypothesized apomorphic for that group.

The supracleithrum of gars has a supracleithral process which is connected to the basicranium via a ligament. Polypterus also has a supracleithral process (Daget, 1950, Jessen, 1972), but Jessen (1972) reports 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 supracleithral processes of Polypterus and gars are homologous. I conclude that the process is apomorphous 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 apomorphous for gars. The cleithrum is connected to the supracleithrum 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 (Jarvick, 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 ledhim 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 which Jessen termed the pontiform process. (M. pro., fig. 15).

(2) Gars and Amia lack a coracoid region which teleosts and chondrosteans have.

(3) The spinal nerves of gars and Amia penetrate the body musculature ventral to the transversely or 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, pp. 259-260) outlined and discussed these points. He concluded that: (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, (2) is refuted by demonstrating that gars have a coracoid canal (cor. can., fig. 15) of the same type as other actinopterygians 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 apomorphy 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 actinopterygian 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 opisthocoelous (fig. 16), a character unique among all actinopterygians except the blenny Andamia (Schaeffer, 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 slerotomic 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 intra- 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 apomorphous 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 last 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 apomorphous relative to the undifferentiated neural spines of Amia and gars; (2) the presence of medial neural spines in Amia is intermediate between teleosts (with medial uroneurals =neural spines) and gars; (3) numerous ural centra, hypurals and epurals are a primitive feature of actinopteryians; (4) the fused hypural-ural centra in Amia is apomorphous 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 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 hemal spines of Amia is apomorphous 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 last 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 which 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 non-synapomorphous, thus eliminating them from considerations of relationship.

Figure 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) and Gardiner (1960, 1963, 1967). The monophyly of halecostomes is corroborated by 14 synapomorphies (characters 1-13, fig. 17a). The monophyly of neopterygians is corroborated by 6 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 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 figure 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 relationships of the fossil semionotid genus Lepidotes, and figure 18a, the corroborating observations forwarded by Patterson (1973) that Lepidotes is a halecostome. Figure 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 which have independently arisen within both the Halecomorphi (amiids) and the Teleostei (Recent groups, see Patterson, 1975 and discussion above).

Figure 19 summarized 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.) 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.

Systematic Accounts

Division Ginglymodi Cope, 1871

Holostei Müller, 1845 p. 119 (in part)

Ginglymodi Cope, 1872, p. 328

Rhomboganoidei Jordan and Evermann, 1896, p. 108

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

Lepidosteoidei Goodrich, 1909 , p. 340

Orthoganoidei Zittle and Koken, 1911, p. 105

Lepisosteiformes Hay, 1929, p. 701 (in part)

Lepidosteiformes Berg, 1940, p. 211

Semionotidea Romer, 1966, p. 353 (in part)

Lepisosteida Matsubara, 1955, p. 170

Lepisostei Suttkus, 1963, p. 61

Diagnosis. The ginglymods differ from all other actinopterygian fishes in the synapomorphous characters shown in figure 19. The more obvious for identification being: 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 parhypurals, hypurals, epineurals, and ural centra, and 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. Pelvic 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 epipeural ribs which 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 basiooccipital, paired exoccipitals, prootics, sphenotics, sphenoids, and a medial orbitosphenoid. Neurocranium lacking a dermal or endochondral intercalar, epiotics, or basisphenoid. Interorbital system 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. Endo- 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 retroarticular. Lateral posterior end of lower jaw overlain by the dermal angular. Hyoid arch without a basihyal and visceral arch and without a fourth infrapharyngobranchial. A long series of paired primary basichyal toothplates. A single highly vascularized swimbladder. Connus arteriosis with seven tiers of eight valves, no bulbous arteriosis. 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, p. 154) from China is a belonid not a gar as reported by Wagner (1912, p. 734). ?*Lepisosteus alessandrii* Ameghino (1898) from Argentina is listed by Pascual (1970) as an improbable member of the genus. *Litholepis adamantinus* Rafinesque (1818a, p. 447) is a mythical fish drawn by J. J. Audubon (Suttkus, 1963, p. 69).

Etymology. From the Greek *ginglymos*, a hinge joint. Referring to the mode of articulation of the opisthocoelus vertebrae.

Family Lepisosteidae Cuvier, 1825

Lepisosteidae Cuvier, 1825, p. 2, 307.

Lepidostei Agassiz, 1832, p. 140. Fitzinger, 1873, p. 52.

Sauroides Agassiz, 1843, p. 2;

Lepidosteinii Müller, 1844, p. 208. Carus, 1875, p. 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, p. 34

+Trichiuridea sagittidens Winkler, 1876, p. 31.

+Pneumatosteus nahunticus Cope, 1869, p. 242; 1875, p. 31. Eastman, 1900a, p. 68.

+Lepisosteus knieskerni Fowler, 1911, p. 150.

+Atractosteus emmonsi Hay, 1929, p. 709 (based on Emmons, 1858, p. 244).

+Paralepidosteus praecurser Casier, 1961, p. 42.

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

Lepisosteus Lacépède

Lepisosteus Lacépède, 1803, p. 331 (type species L. gavialis by subsequent designation, Jordan and Evermann, 1896, p. 109).

Sarchirus Rafinesque, 1818a, p. 418 (type species S. vittatus by subsequent designation, Jordan, 1877, p. 9).

Cylindrosteus Rafinesque, 1820, p. 72 (type species C. platostomus by subsequent designation, Jordan, 1877, p. 11).

Lepidosteus (Lacépède): Koenig, 1825, p. 12; Agassiz, 1843, p. 2.

Diagnosis. Gars with an ectopterygoid-premaxillary articulation on the premaxillary process, without enlarged dermopalatines fangs, with projecting ridges above and below the articular socket of the supracleithrum. The frontal bone elongate anteriorly and posterio-laterally, 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 tooth plates on the first infrapharyngobranchial (fig. 22) and the first three hypo- and ceratobranchials.

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

The following nominal species are Lepisosteus species indeterminate:

+Clastes cycliferus Cope, 1873, p. 634; 1877b, p. 40; 1884, p. 54. Woodward, 1895, p. 445. Merrill, 1907, p. 8.

+Lepidosteus cycliferus (Cope): Eastman, 1900a, p.68; Cockrell, 1908, p. 163.

+Lepisosteus cycliferus (Cope): Hay, 1902, p. 337; 1929,

+Lepidosteus longus Lambe, 1908, p. 13.

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, L. 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, p. 43; 1969, p. 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 (MCZ00000) is an incomplete frontal (figures 20a, 23a). Paratypes include two fragmentary frontals (MCZ 00000), two dermoperotics (MCZ 00000, fig. 23b), one preopercular (MCZ 00000 , figs. 23c), 17 infraorbitals (MCZ 00000), three parietals (MCZ 00000, 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 morphometrics or meristics were obtainable.

All premaxillaries from the Hell Creek formation have a double row of premaxillary teeth, but at present 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 narrow and elongate, with rounded enameloid tubercles. Circumorbitals with enameloid, condition of the dorsal circumorbital and relationship of the dermosphenotic to the orbital margin unknown. Number of supratemporals per side unknown. Supracleithrum with long bony process on the ventral side of the articular facet (fig. 24a).

Frontal shape like that of other Lepisosteus (fig. 20a). Frontal with rows of rounded enameloid tubercles along the bony ridges. Shape and enameloid pattern of the dermopterotic and parietal compared to other Lepisosteus shown in figures 25a and 27a respectively.

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 preopercular. In addition, *L. opertus* has sheets of enameloid on the parietals and dermosphenotics and elongate infraorbitals and a *Lepisosteus* supracleithrum whereas *A. occidentalis* has rounded enameloid tubercles on the dermosphenotic, square infraorbitals, and a supracleithrum 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)

Figures 20b, 25b, 27b, 29b, 31, 32

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

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

Diagnosis. Differs from all other Lepisosteus in that the width of the opercular ans subopercular exceed the distance from the margin of the opercular aparatus and the suborbitals anterior to the medio-posterior orbital margin whereas in all other Lepisosteus the width of the opercular and subopercular does not exceed this distance.

Type. AMNH 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 figure 31. Meristic data are shown in Table 2.

Presence of 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 post orbital 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 dermopterotic, parietal, and opercular shown in figures 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 interconnected 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 posterior of the parietals and dermopterotics, and dorsal half of the opercular and in having large rounded enameloid, tubercles on other parts of these bones whereas fimbriatus and Recent Lepisosteus less enameloid is thinner, usually disconnected tubercles (reduced in many 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.

Lepisosteus platostomus Rafinesque

Shortnose Gar

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

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

Lepisosteus albus Rafinesque, 1820, p. 73.

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

Cylindrosteus scabiceps Fowler, 1910, p. 607. Jordan, Evermann and Clark, 1930, p. 37.

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

Diagnosis. Differs from all other Lepisosteus 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. oculatus, L. platyrhinchus, and L. fimbriatus). Differs from L. opertus in having enameloid ridges which are thin and usually disconnected into oblong tubercles whereas L. opertus has wide continuous tubercles.

Type. No type material was collected by Rafinesque.

Description and comparisons. A small gar without flank stripes or belly pigmentation in adults. A typical skull is shown in figure 33. Meristic counts are shown in Table 2 whereas various morphometric measurements expressed as ratios of dorsal head length are shown in Tables 3 and 4.

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

Premaxillary process with ridges for the articulation of the 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, the dorsal circumorbital not enlarged, the dermosphenotic included in the orbital margin, three circumorbitals including the dermosphenotic forming the posterior orbital margin. Three lacrimels. Suborbitals not numerous, the ventro-posterior marginal suborbitals distinctly larger than those of the internal mosaic. Two or four supratemporals on each side of the midline. Supracleithrum with projections above and below the articular facet, its shape shown in figure 24b.

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

First basihyal toothplate paired. Gill rakers small and pearshaped (fig. 21a), and not numerous (Table 2). A single row of medial toothplates on the first arch. A single complete row of medial toothplates on the second and third lower arch elements and two complete rows on the fourth arch, (fig. 34a), a single row of medial toothplates on the first infrapharyngobranchial and 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._ _platyrhinchus_ in number of lateral line scales (59-65 in _platostomus_, 53-59 in _oculatus_ and _platyrhinchus_) and head color pattern (blotched in _oculatus_ and _platyrhincus_ plain in _platostomus_).

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 Yueno and Miller (1963) as *L. platyrhincus*.

+ *Lepisosteus indicus* (Woodward)

Figures 20e, 36

Belonstomus (?) *indicus* Woodward 1890, p. 23; 1895, p. 439.
Lepidosteus indicus Woodward 1908, p. 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, 12186) figured by Woodward 1908.

Type Locality. Lameta Beds, Dongargoan, Madhya Pradesh, Central Province, India

Formation and Age. Lameta Formation, Upper Cretaceous.

Description and comments. The skull (B.M.N.H.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). The right frontal is 160 mm in length, the left frontal is too fragmentary to measure. Both premaxillaries are partly preserved. The ascending process of the premaxillary makes up a significant part of the snout roofing bones and is typically gar-like and carries part of the supraorbital canal. The left lower jaw is exposed with its inner surface showing. It is 181 mm from the tip of the retroarticular to the broken anterior end. The posterior articular series is fragmentary. The articular-retroarcticular articulating surface is concave and similar in shape to that in other gars. The inner surface of the dentary is broken, exposing the meckelian groove. Both large and small plicidentine teeth are preserved. Part of the right infraorbital chain are preserved. Woodward (1908, p.4) incorrectly identified this series of three infraorbitals as the "palato-pterygoid arcade." Additional preparation revealed articulations between the infraorbitals and the infraorbital sensory canal line. The infraorbitals lack bony ridges or enameloid. One circumorbital was identified. The fragmentary hyomandibular is similar to that of other gars. The parasphenoid is partly preserved and lies between the two frontals. The left ectopterygoid is preserved. There are fragments of both the vomers and dermopalatines. There is no indication of dermopalatine dentition. One bone is preserved which fits into the position of the supraorbital on the frontal concavity. This supraorbital does not carry the infraorbital canal (like that of Lepisosteus but not Atractosteus). One canal bearing bone has been tentatively identified as a circumorbital. It is located to the left of the partly preserved hyomandibular.

Etymology. The trivial name indicus refers to the country of occurence.

Lepisosteus osseus (Linnaeus)

Longnose Gar

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

Esox osseus Linnaeus, 1758, p. 313.

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

Lepisosteus gavialis Lacépède, 1803, p. 333.

Sarchirus vittatus Rafinesque, 1818a, p. 419.

?*Lepisosteus stenorhynchus* Rafinesque, 1818b, p. 447 (listed by Suttkus, 1963, as a doubtful synonym).

Lepisosteus oxyurus Rafinesque, 1820, p. 73.

Lepisosteus longirostris Rafinesque, 1820, p. 74.

?*Sarchirus argenteus* Rafinesque, 1820, p. 86 (listed by Suttkus 1963, as a doubtful synonym).

Lepidosteus osseus: Agassiz, 1843, p. 2; Günther, 1870, p. 330.

Lepidosteus semiradiatus Agassiz, 1843, p. 2.

Lepidosteus gracilis Agassiz, 1843, p. 2.

Lepisosteus huronensis Richardson, 1836, p. 237.

Lepidosteus rostratus Cuvier In Richardson, 1836, p. 238.

Lepidosteus bison De Kay, 1842, p. 271.

Lepisosteus lineatus Thompson, 1842, p. 145.

Macrognathus loricatus Gronow, 1854, p. 148.

Lepidosteus leptorhynchus Girard, 1858, p. 351.

Lepidosteus otarius Cope, 1865, p. 86.

Lepidosteus crassus Cope, 1865, p. 86.

Lepidosteus treculi Duméril, 1870, p. 327.

Lepidosteus mulberti,Dumétil, 1870, p. 228.

Lepidosteus harlani Duméril, 1870, p. 329.

Lepidosteus smithi Duméril, 1870, p. 330.

Lepidosteus ayresii Duméril, 1870, p. 331.

Lepidosteus copei Duméril, 1870, p. 332.

Lepidosteus lesueurii Duméril, 1870, p. 335.

Lepidosteus elisabeth Duméril, 1870, p. 336.

Lepidosteus lamarii Duméril, 1870, p. 337.

Lepidosteus clintonii Duméril, 1870, p. 338.

Lepidosteus troostii Duméril, 1870, p. 339.

Lepidosteus piquotiamus Duméril, 1870, p. 340.

Lepidosteus horatii Duméril, 1870, p. 341.

Lepidosteus thompsoni Duméril, 1870, p. 342

Lepidosteus louisianensis Duméril, 1870, p. 343.

Lepidosteus osseus: Suttkus, 1963, p. 79.

Diagnosis. *Lepidosteus oseeus* 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 broken snout on deposit in 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 figure 35. Morphometrics expressed as ratios of dorsal head length shown in Table 3 and 4.

Color pattern of adults varying with environmental conditions (Suttkus, 1963, p. 77). Juveniles with continuous mid-dorsal stripe missing in adults whose dorsum is darkened by general melanophore development. Flank stripe of juve eniles continuous from base of caudal fin through the eye onto the lower jaw. Flank stripe of juveniles serrate on upper margin. Adult flank stripe either missing or reduced to a series of 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 the lower jaw, this pigment extending from the symphysis to the branchiostegals. Isthmus with or without scattered pigment of variable intensity. One belly stripe per side of juveniles extending from the pectoral base to the anal fin where the stripes merge to form one stripe on the ventrum of the 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 two to five transverse rows of transverse 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 the orbital margin, three circumorbitals comprising the 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 the midline. Supracleithrum with bony projections above and below the articular facet, its shape distinctive compared with other Lepisosteus (fig. 24c).

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

Differs from L. oculatus, L. platyrhincus, and L. fimbriatus in that L. osseus has two to four teeth in the outer row of the premaxilla whereas the other three species have a single medial tooth in the outer row (rarely two in platyrhincus). Also differs from L. oculatus and L. platyrhincus in that osseus lacks large pigment blotches on the 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 the head and fused first basihyal toothplates. Differs from *L. platostomus* and *L. opertus* in that *L. osseus* has an incomplete outer row of premaxilla teeth wereas the above species have a complete outer row of teeth. Also differs from *L. platostomus* in juvenile and adult color pattern and from *L. opertus* in that *opertus* has wide interconnected enameloid ridges on the parietals and dermopterotics whereas *osseus* has thin continuous tubercles or series of round or oblong tubercles on these bones which 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 fimbriatus* Wood

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

Lepidotus fimbriatus Wood, 1846, pp. 6, 122. Woodward, 1895, p. 442.

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

Lepidosteus maximiliani Vasseur, 1876, p. 295.

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

Diagnosis. Differs from all *Lepisosteus* except *L. oculatus* and *L. platyrhincus* in that *L. fimbriatus* as the two other species have a single medial tooth 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 dermopteryotic, parietals, and supracleithrum. 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 enameloidon the dermopteryotics, parietals, frontals, and supratemporals whereas *L. fimbriatus* has elongate to oval enameloid tubercles on these bones.

Types. B.M.N.H.P. 25252 (partial dentary) and 25254 (opercular).

Formation and age. Known from most freshwater Eocene and lower Oligocene 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 figure 37. No meristics or morphometrics were obtainable.

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

Frontal shape like other relatively short-nosed *Lepisosteus* (fig. 20). Shape and enameloid pattern of the dermopterotic, parietal, and opercular compared to other *Lepisosteus* shown in figures, 26 b, 28b, 30a. Enameloid pattern and shape of other bones shown in figure 37. Vertebral centrum shape 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 (1959, 1874a, b) 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

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

Lepisosteus latirostris Girard, 1858, p. 352 (placed in synonomy with *C. castelnaudii*= *L. oculatus* by Jordan, Evermann, and Clark, 1930, p. 37).

Lepisosteus oculatus Winchell, 1864, p. 183. Suttkus, 1963, p. 71.

Cylindrosteus productus Cope, 1865, p. 86.

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

Cylindrosteus bartonii Duméril, 1870, p. 347.

?*Cylindrosteus zadocki* Duméril, 1870, p. 353.

Lepisosteus platostomus Jordan and Everman 1896, p. 110 (in part, *L. oculatus* listed as synonym of *L. platostomus*).

Cylindrosteus castelnaudii Jordan, Everman and Clark, 1930, p. 37 (in part).

Lepisosteus productus: Hubbs and Lagler, 1943, p. 76. Eddy, 1957, p. 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. 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 Figure 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 continues in young, usually broken into a series of blotches in adults, running from the caudal peduncle anteriorly through the eye onto the lower jaw where it fuses with the preopercular stripe. Preopercular stripe usually continuous, occasionally broken. Retroarticular spot present and may or may not contact the flank stripe in front of the 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 the isthmus. One belly stripe per side, these stripes stripes usually interconnected by reticulate pigment blotches between the stripes. Some adults with uniformly dark belly pigment which obliterates the belly stripes other adults 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 the pectoral fin-base dark. Dorsal, anal, and caudal fins with varying numbers of pigment blotches.

Premaxilla with ridges on its process for articulation of the ectopterygoid and with a single medial tooth in the outer tooth row. Dermopalatine with two tooth rows, the inner row of adults not enlarged as fangs. Six to eight infraorbitals. Eight to nine circumorbitals with the dorsal circumorbital not enlarged and the dermosphenotic incorporated into the orbital margin. Three circumorbitals forming the posterior margin 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 the midline. Supracleithrum with projecting ridges above and below the 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 figure 20g. Shape and enameloid patterns of the pterotic, parietals, and opercular shown in figures 26c, 28c, and 30b respectively.

First basihyal toothplate fused. Gill rakers small and pear-shaped (figure 21c) numbering 15 to 24 on the first arch outside row (Table 2). Medial toothplate pattern shown in figure 34c. Medial toothplate running on the 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. 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 the 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 eastward to Central Texas (Suttkus, 1963).

Lepisosteus platyrhincus De Kay

Florida Spotted Gar

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

Lepisosteus platyrhincus De Kay, 1870, p. 355. Suttkus, 1963, p. 83.

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

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

Cylindrosteus megalops Fowler, 1910, p. 609. Jordan, Evermann, and Clark, 1930, p. 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.

Description and comparisons: Lepisosteus platyrhincus is a medium sized gar (to 1,330 mm total length; Hammett and Hammett, 1936) which is usually darkly pigmented. A skull is shown in figure 39. Meristics taken in this study and reported by Suttkus (1963) shown in Table 2. Morphometrics taken from a small series 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 "immaculate" to very dark individuals from the same localities, Suttkus, 1963). Dorsal stripe continuous in juveniles, adults with a uniform dark or mottled dorsum. Flank stripe in young from the base of the caudal fin through the eye, and to the tip of the lower jaw. Flank stripe of adults usually broken into a series of darker and lighter blotches. Juveniles with a stripe between the dorsal and flank stripes from the nape to one-half the distance between the pectoral and pelvic fins. Belly with one or two belly stripes per side, these stripes fusing at the anal fin to form one stripe on the caudal peduncle. Most individuals with belly mottled between the belly stripes. Head with large pigment blotches on the dorsum. Preopercular and retroarticular stripes present, fused with each other, and usually fused with the flank stripe just anterior to the eye. Gular region usually solidly pigmented, isthmus mottled. Pectoral fin base pigmented. Three to five transverse rows of pigment blotches on the 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).

Maxilla with a single medial tooth on the outer tooth row (occasional individuals will have two teeth on one side, one tooth on the other). Dermopalatine of adults without enlarged fangs. Eight to ten circumorbitals, dorsal circumorbital not enlarged, dermosphenotic included in the orbital margin. Three circumorbitals comprising the posterior orbital margin, including the dermosphenotic. Six to seven infraorbitals. Three lacrimals. Suborbitals not numerous, margin suborbitals larger than the internal mosaic. Supracleithrum with bony projections above and below the articular facet, the shape of the supracleithrum shown in figure 24f. Shape and enameloid pattern of the dermopterotic, parietal, and opercular shown in figures 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*). Also 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 enameloid tubercles on the dermopteryotics 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.

Genus *Atractosteus* Rafinesque

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

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

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

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

Diagnosis. Gars with large laterally compressed gill rakers which are convoluted on their dorsal edges (fig. 21), lacking medial toothplates on the first three hypo- 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 articular socket of the supracleithrim without projecting ridges, and in having enlarged dermopalatine fangs as adults.

Etymology. A compound masculine nominative derived from the Greek *atractos* (=spindle) and Latin *osseus* (=boney)

The following names are considered here as *Atractosteus* species indeterminent:

Clastes pastulosus Sauvage, 1897, p. 94 (Cret., Portugal).

Atractosteus lapidosus Hay, 1919, p. 110, 1923, p. 375 (? *A. spatula*, Pleistocene, Fla.).

+Atractosteus strausi (Kinkelin)

Figures 40-46, 47a, 49a, 51a, 53a

Lepidosteus strausi Kinkelin, 1884, p. 244; 1903, p. 25-26
Andreae, 1893, p. 7; 1894, p. 359. Woodward, 1895, p. 444

Diagnosis. Differs from all Atractosteus except A. tropicus in that A. strausi has sheets of enameloid on the frontals, parietals, dermopteryotics 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 the 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 during this study.

Formation and age. Messel Formation, Darmstadt, Germany, Eocene.

Description and comparisons. Atractosteus strausi is an Eocene gar attaining large size. A whole specimen (AMNH P.4626) is shown in figure 40. A closeup of this skull, two other skulls (AMNH 33839, 33856), and accompanying outline drawings of these skulls are shown in figures 41-46 respectively.

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 and not as numerous as those of the spatula group. Two supratemporals on each side of the midline.

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

Atractosteus strausi differs from *A. simplex* in that *A. strausi* 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. strausi* has a narrow dorsal circumorbital and 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. A patronym.

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

Atractosteus tropicus Gill

Tropical Gar

Figures 6, 21e, 22b, 476, 496, 516, 54, 55a, 56c

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

Atractosteus belandieri: Duméril, 1870, p. 368

Lepisosteus tropicus: Jordan and Evermann, 1896a, p. 111; 1896b, p. 227. Miller, 1954, p. 230. Suttkus, 1963, p. 70.

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

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 figure 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 the caudal peduncle to the eye where it fuses with general head pigmentation.

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

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

Premaxilla without ridges on the arm, ectopterygoid articulating with the premaxilla proper. Premaxilla with two complete tooth rows. Dermopalatine with two tooth rows, the inner row of adults enlarged as dermopalatine fangs. Six to eight infraorbitals. Nine to ten circumorbitals, the single dorsal circumorbital not enlarged, the dermosphenotic incorporated into the orbital margin. Three circumorbitals on the posterior orbital border including the dermosphenotic. Three lacrimals. Suborbitals not numerous, those of the ventral-posterior border larger than the internal mosaic. Two or three supratemporals on each side of the midline. Articulatory facet of the supracleithrum without ridges, its shape shown in figure 55a.

Dorsal dermal roofing bones with sheets of enameloid. Enameloid reduced on infraorbitals and the opercular series. Shapes and enameloid patterns of the dermopterics, parietals, and opercular shown in figures 476, 49b, and 51b respectively.

First basihyal toothplate paired. Gill rakers laterally compressed, convoluted on dorsal edge and sitting on basal plates (figure 21e). Gill rakers numbering 57-62 on outside of first arch (Table 2). Medial toothplate missing on first three hypo- and cerate-hyals and first infraphryngobranchial, reduced to a single incomplete row on fourth hypo- and ceratobranchials and second infraphryngobranchial (see figure 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 occurence in Middle America.

Other comments. See comments for *A. spatula* from Lake Nicaragua.

+Atractosteus simplex (Leidy)

Figures 47c, 49c, 51c, 53c, 55b, 57, 58

Lepidosteus glaber Marsh, 1871, p. 105 (name only). Cope, 1874, p. 441 (listed not recognizable). Woodward, 1895, p. 444. Eastman, 1900a, p. 67 (nomen dubium). Cockerell, 1908, p. 163.

Lepidosteus simplex Leidy, 1873a, p. 73; 1873b, p. 189. Woodward, 1895, p. 444. Eastman, 1900a, p. 74. Cockerell, 1908, p. 163; 1909, p. 796.

Clastes glaber: Cope, 1873, p. 634; King, 1878, p. 376, p. 405.

Lepidosteus aganus Cope, 1877b,p. 40. Cockerell, 1908, p. 163.

Clastes integer Cope, 1877b,p. 41. Merrill, 1925, p. 361.

Lepisosteus glaber: Hay, 1902, p. 377; 1929, p. 708.

Lepisosteus simplex: Hay, 1902, p. 377; 1929, p. 708. Hussarkof and Bryant, 1919, p. 195.

Lepisosteus aganus: Hay, 1902, p. 377; 1929, p. 708. Stromer, 1925, p. 361.

Lepisosteus integer: Hay, 1902, p. 377; 1929, p. 708.

Clastes aganus: Merrill, 1907, p. 7.

Lepidosteus integer: Loomis, 1907, p. 358; Cockerell, 1908, p. 163; Stromer, 1925, p. 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 which are transversely grooved. *Atractosteus simplex* differs from all other *Atractosteus* (where 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 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 which excludes the dermosphenotic from the orbital margin and in that *A. spatula* has minute round enameloid tubercles and *A. tristoechus* lacks enameloid whereas *A. simplex* has larger rounded tubercles.

Types. USNM 2174, one basioccipital and three vertebrae. USNM 21173, basioccipital-parasphenoid, three vertebrae, 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, Wasatch, and Green River Formations, Lower Eocene.

Description and comparisons. The type and co-type resemble the bones associated with more complete AMNH and USNM specimens. The skull of AMNH 4302 is shown in figures 57 and 58. Meristic data collected by Eastman (1900a) is shown in Table 2. Morphometrics from this skull: DHL - 139.6 mm; PS - 72.4 mm; POr - 54.2 mm; OpW - 18.6 mm; LLJ - 86.6 mm; OrD - 17.8 mm. Comparisons with other gars of these measurements expressed as proportions of dorsal head length are shown in Tables 3 and 4.

Two complete rows of premaxillary teeth (USNM 16712). The dermopalatine has an inner tooth row of enlarged dermopalatine fangs (USNM 16712, AMNH 4302). There are six infraorbitals (AMNH 4302, 4308) and two lacrimals (AMNH 4302). There are eight circumorbitals (AMNH 4302), the dorsal circumorbital is thin, and the dermosphenotic is included in the orbital margin. Two circumorbitals make up the posterior border of the orbit including the dermosphenotic. There are relatively few suborbitals and the margin suborbitals bordering the preopercular are distinctly larger than the internal mosaic. Two supratemporals present on each side of the midline (AMNH 4302, 4308), Supracleithrum is without distinct projecting ridges above and below the articular facet. The shape of the supracleithrum is shown in figure 55b.

Frontal shape typical of the genus (fig. 53c), and most similar to that of *A. strausi*. The shape and enameloid pattern of the dermopterotic, parietal, and opercular shown in figures 47c, 49c, and 51c respectively. Infraorbital enameloid reduced relative to *A. strausi* and *A. tropicus*. Enameloid on other skull roofing bones missing of reduced to small round or slightly oblong tubercles. Vertebrae of large specimens distinctly subtriangular. Scales smooth.

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

+*Atractosteus africanus* (Arambourg and Joleaud)

Figures 16, 59

Paralepidosteus africanus Arambourg and Jouleaud, 1943, p. 42. Casier, 1961, p. 41. Patterson, 1973, p. 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.

Descriptive comments. N.155 is a large abdominal vertebra, 41 mm along the ventrum of the centrum. Transverse processes not preserved, ventral ridges wide, incomplete neural arches. N.27 is a large abdominal vertebra (33 mm centrum length, 39.6 mm centrum width, and 35.8 mm maximum centrum width) subtriangular, with ventrally directed transverse processes and two widely spread ventral ridges. N.29 is a small (13 mm centrum length) almost complete abdominal vertebra with ventral ridges like N.27. N.28 is a posterior abdominal vertebra with strongly downturned transverse processes measuring 19 mm in centrum length. N.30 is a caudal vertebra, 25 mm in centrum length with a rectangular articulating surface. The infraorbital, N.37, has a random pitted pattern of dermal ornamentation, not organized into radiating ridges like other Atractosteus. This bone was interpreted by Arambourg and Joleaud (1943) as a part of the dentary. It is interpreted here as an infraorbital because: (1) in all other Atractosteus the last infraorbital has two closely situated rows of outwardly directed teeth and the outer row of teeth is not much larger than the inner row, a characteristic of N.37; and (2) the bone is flattened like a typical posterior Atractosteus infraorbital.

Etymology. The trivial name africanus refers to the continent of occurence.

+Atractosteus occidentalis (Leidy)

Figures 38c, 48a, 55c, 60

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

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

Clastes occidentalis Cope, 1884, p. 52.

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

Lepisosteus haydeni: Cockerell, 1908, p. 136.

Lepidotes occidentalis: Osborn, 1902, p. 11. Hatcher, 1905, p. 67. Lambe, 1907, p. 179. Peale, 1912, pp. 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 dermopteryotic whereas *occidentalis* has a thick dorsal circumorbital (which could presumably restrict the dermosphenotic from the orbital margin), and high rounded enameloid tubercles on the dermopteryotic. Differs from *A. atrox* in that *atrox* has boney ridges which are transversely striated on the frontals and dermopterotics whereas *occidentalis* has non-striated boney 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 whereas *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 from disarticulated material only. Large premaxillae 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 and presumably excluded the dermosphenotic from the orbital margin. Those suborbitals which can be distinguished from *L. opertus* are small and have a few scattered and rounded enameloid tubercles on the boney ridges. Number of supratemporals per side undeterminable. Supracleithrum with simple articular facet and the axis of the bone straight. Supracleithrum most similar in shape to *A. atrox* (fig. 55).

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

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

Other comments. *A. occidentalis* occurs in the same localities as *L. opertus*. Only those bones which 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 await 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)

Figures 48b, 50a, 52a, 53d, 55d, 61, 62

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

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

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

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

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

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

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

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

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

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

Formation 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 4755 (figs. 61, 62) and MCZ 5168 (a complete specimen with crushed skull). Meristics reported by Eastman (1900a) shown in Table 2. Morphometrics taken from the USNM 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 shown in Tables 3 and 4.

Two complete [illegible] teeth. Dermopalatine not observable. [illegible]s. Number of circumorbitals [illegible] circumorbital enlarged and pr[illegible] enotic from the orbital marg[illegible] is small, but relative size of ma[illegible] and the internal mosaic not determinable. Three supratemporals on each side of the midline. Supracleithrum with simple articular facet, without distinct projecting ridges. Shape of the supracleithrum most similar to *A. spatula* and *A. tristoechus* (fig. 55).

Frontal shape similar to others in the genus (fig. 53d). Shape and enameloid pattern of the dermopterotic.

parietal, and opercular shown in figures 48b, 50a and 52a respectively. Differs from A. strausi, A. tropicus, and A. simplex in having an enlarged dorsal circumorbital which excludes the dermosphenotic from the orbital margin. Differs from A. spatula in that atrox has the enameloid pattern stated above whereas spatula has minute 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).

Formation 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 4755 (figs. 61, 62) and MCZ 5168 (a complete specimen with crushed skull). Meristics reported by Eastman (1900a) shown in Table 2. Morphometrics taken from the USNM 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 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 and presumably excluded dermosphenotic from the orbital margin. Preserved suborbitals small, but relative size of marginal suborbitals and the internal mosaic not determinable. Three supratemporals on each side of the midline. Supracleithrum with simple articular facet, without distinct projecting ridges. Shape of the supracleithrum most similar to *A. spatula* and *A. tristoechus* (fig. 55).

Frontal shape similar to others in the genus (fig. 53d). Shape and enameloid pattern of the dermopterotic.

parietal, and opercular shown in figures 48b, 50a and 52a respectively. Differs from *A. strausi*, *A. tropicus*, and *A. simplex* in having an enlarged dorsal circumorbital which excludes the dermosphenotic from the orbital margin. Differs from *A. spatula* in that *atrox* has the enameloid pattern stated above whereas *spatula* has minute 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).

Atractosteus spatula (Lacépède)

Alligator Gar

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

Lepisosteus spatula Lacépède, 1803, p. 333.

Lepisosteus ferox Rafinesque, 1820, p. 73. Kirtland, 1844, p. 18.

Lepisosteus belandieri Girard, 1858, p. 353.

Atractosteus lucius Duméril, 1870, p. 366.

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

Litholepis adamantimus Rafinesque: Jordan, 1877, p. 16.

Litholepis spatula: Jordan, 1877, p. 16.

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

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

Diagnosis. *Atractosteus spatula* differs from *A. tropicus*, *A. strausi*, *A. simplex*, and *A. atrox*, in dermal roofing bone enameloid patters (figs. 47-52), from *A. tropicus* in lateral line scale count (58-62 in *A. spatula*, 51-56 in *A. tropicus*), number of predorsal scales (49-54 in *A. spatula*, 43-48 in *A tropicus*). *Atractosteus spatula* differs from *A. tristoechus* in lacking 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 deposited at the Muséum National d'Histoire Naturelle, Paris, France.

Description and comparisons. *Atractosteus spatula* is the largest of living gars reaching a maximum reported length of over 3 meters and weight of 137 kilos (Suttkus, 1963). Meristic counts are shown in Table 2. Skull measurements as expressions of ratios of dorsal head length are shown in Tables 3 and 4.

Color pattern descriptions have been given by Suttkus (1963) for adults and juveniles and by Moore et al. (1973) for a small juvenile specimen. Juveniles with flank stripe which fades 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 a pair of dark dorsal stripes bordering a medial light stripe, these stripes running from the back of the head to the base of the caudal fin and fading with age. Fins of juveniles with pigment blotches, some adults with blotches. The fin rays are usually brown. Adults with dark brown to tan dorsums, fading ventrally to a white or yellowish belly. Throat region speckled.

The premaxilla with two complete rows of teeth. Dermopalatine fangs as large as infraorbital fangs in adults. Vomer with a 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 without enameloid. Approximately eight circumorbitals. The dermosphenotic excluded from the orbital margin. Many suborbitals approximately 10 more along the posterior border, including the "dermohyals." Three posttemporals on each side of the 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, vertebrae with wide ventral ridges. Anterior scales with ridges, posterior scales smooth.

Gill rakers ornate, sitting on basal plate and laterally compressed (fig. 21f). Medial tooth plates missing on first three arches, reduced to a single incomplete row on fourth arch and 3-4 rows on fifth ceratobranchial (fig. 56a), first basihyal toothplates are 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 Lake Nicaragua (TU388). Presence of absence of this species between the two disjunct populations unknown.

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

Atractosteus tristoechus (Bloch and Schneider)

Cuban Gar or Manjurai

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

Esox tristoechus Bloch and Schneider, 1801, p. 395.

Lepidosteus manjuari Poey, 1854, p. 273.

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

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

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

Lepisosteus tristoechus: Suttkus, 1963, p. 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 circumorbital which 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 figure 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, the ectopterygoid articulating with the premaxilla proper. Two complete rows of premaxilla teeth. Dermopalatine with two teeth rows, the inner row enlarged as fangs. Three to five infraorbitals. Eight to nine circumorbitals, dorsal circumorbital enlarged excluding the dermosphenotic from the orbital margin. Three circumorbitals lining the posterior orbital margin including the dorsal circumorbital. Three lacrimals. Suborbitals numerous, ventral-posterior marginal suborbitals only slightly larger than the internal mosaic. Three or occasionally five supratemporals on each side of the midline. Articular facet of the supratemporal simple, without projecting ridges, devoid of enameloid. Shape of the supracleithrum 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 figures 48d, 50c, and 52c respectively. Frontal shape shown in figure 53f.

First basihyal toothplate paired. Gill rakers laterally compressed, convoluted on dorsal edge, and 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 hypo- and ceratobranchials and first infraphryngobranchial (fig. 56b), reduced to a single incomplete row on fourth arch and second infraphryngobranchial.

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 presented in the foregoing descriptions of the genera and species of gars are discussed below and conclusions are drawn as to their relative apomorphous or plesiomorphous nature. After this discussion, four phylogenetic hypotheses will be presented as a summary, two for each genus. The first will incorporate only the Recent species whereas the latter will place the fossil morphotypes at the level their preserved characters allow analysis. The rationale of this approach rests primarily on the inherent incompleteness of the fossil specimens I have 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) in the case of 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 the elucidation of the relationships of the fossil morphotypes. Thus, much of the analysis of fossil gars concerns the discovery of preservable characters which are correlated with synapomorphies which are less ambiguous. Coupled with the above reasoning is the problem of sample size. Analyzable fossil gars are rare. In some cases, such as *L. opertus* and *A. occidentalis*, the morphotype is represented only by disarticulated remains and many of these remains are not definitely assignable to one or the other species. In the case of *A. africanus*, the entire morphotype is represented by one infraorbital and a few vertebrae. In other cases, such as *L. indicus* and *A. atrox*, the morphotype is represented by one or two skulls. Because of the low number of specimens available for analysis, intraspecific variation can not 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 than the *Lepisosteus* gars. 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 in very thin. In *Atractosteus* the lateral boundry 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. There differences between *Lepisosteus* and *Atractosteus* gars are reflected in the shape of the frontal bones of the two genera. Because the *Lepisosteus* snout is more elongate, and thus relatively more apomorphous than the *Atractosteus* snout, the *Lepisosteus* frontal shape is hypothesized the more apomorphous of the two types of frontal shapes.

Gill Rakers. There are two types of gill rakers found among Recent gars. The first, found in *Lepisosteus* gars, are not numerous, are pear-shaped and studded with many relatively large teeth. These gill rakers are similar to those of *Amia 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 first three arches and these toothplates are reduced to a single incomplete row on the fourth arch (fig. 56). *Lepisosteus* gars have these toothplates, albeit reduced as compared with those of other neopterygians such as *Amia* 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 premaxillary articulate with each other. In *Atractosteus*, the ectopterygoid articulates immediately posterior to the nasal foramen on the premaxillary proper. This is essentially the same type of articulation found in other actinopterygians (although, of course, the autapomorphous premaxillary process of gars produces a ectopterygoid-premaxillary association not similar to that of other actinopterygians). The articulation in *Lepisosteus* differs in that the ectoptopterygoid articulates with the premaxillary process and not with the premaxillary 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 (Suttkus, 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* and *L. cuneatus*; *A. strausi* and *A. tropicus*). In all *Lepisosteus* gars except *L. indicus* there are also large amounts of enameloid on the infraorbitals and preoperculars (in *L. opertus* 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. 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 apomorphous for the genus *Atractosteus*, whereas the retention of this enameloid in primitive *Lepisosteus* gars is considered plesiomorphous.

Supracleithrum. Gars differ from other actinopterygians in having a supraclethrium 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 supracleithrum also differs in the two genera (figs. 24, 55), but the characterization of either as plesiomorphous or apomorphous 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* differs 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 plesiomorphous. Other *Lepisosteus* display a reduction trend in the number of teeth on the outer row. *Lepisosteus osseus* has an intermediate number of 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. osseus* is considered plesiomorphous relative to those in the latter three species.

Ectopterygoid premaxillary 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*. *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 tooth plates is known only in Recent forms. As discussed above, *Lepisosteus* differs from *Atractosteus* in having some medial tooth plates on the first hypobranchials whereas *L. oculatus* and *L. platyrhincus* lack medial toothplates on the first hypobranchial. This condition in the latter species is hypothesized 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 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 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 apomorphous. 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*. *Lepisosteus cuneatus* 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 thin elongate enameloid tubercles or enameloid tubercles present as series of oblong disconnected tubercles on these bones. *Lepisosteus osseus* has less enameloid on the parietals and dermopterotics than other species, except *L. fimbriatus* and *L. indicus* (which lacks enameloid completely). All *Lepisosteus* show a tendency to have small rounded enameloid tubercles on the frontal bones. *Lepisosteus osseus* has reduced the amount of enameloid on the frontal bones to a greater extent that 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*, where the enameloid is missing and the boney ridges are reduced in height. The complete loss of enameloid in *L. indicus* and *A. tristoechus* is considered here as a non-homology.

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.

Relationships Among *Atractosteus* Gars

Dermosphenotic and the circumorbital 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* and *A. strausi* the dermosphenotic is excluded from the orbit by an enlargement of the dorsal circumorbital (the supraorbital) and the orbit is relatively small. 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, the same conditions seen in *A. tropicus*, *A. strausi*, and *A. simplex*. I conclude that the conditions seen in *A. tropicus* and *A. strausi* are plesiomorphic relative to that seen in the *spatula* species group.

Infraorbital enameloid. The only two species of *Atractosteus* which retain 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, as do the infraorbitals of the articulated skulls of A. atrox and A. simplex. The single preserved infraorbital of A. africanus lacks enameloid. Enameloid is present on the infraorbitals of all Lepisosteus and since large amounts of enameloid on dermal bones seems a primitive actinopterygian characteristic, I interpret the presence of infraorbital enameloid as plesiomorphous. Thus the lack (or virtual lack of) enameloid of A. africanus, A. occidentalis, A. simplex, A. atrox, A. spatula and A. tristoechus is considered 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, A. strausi (and L. opertus) which have broad flat interconnected enameloid tubercles running on top of the bony ridges of the dermopterotics, parietals and other roofing bones. This hypothesis is not refuted by the observation that many chondrosteans have essentially the same type of enameloid. A. atrox has a unique enameloid pattern. Atractosteus occidentalis and A. simplex have reduced numbers of round or oblong tubercles which are considered relatively plesiomorphic to the minute enameloid tubercles of A. spatula. Atractosteus tristoechus lacks enameloid completely and is hypothesized to have the most apomorphous condition within this group.

Color pattern. Atractosteus tropicus juveniles have all the color pattern characters considered plesiomorphous 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 as apomorphous relative to the patterns of A. tropicus.

Summary of relationships and discussion. The four phylograms presented below in figures 65 to 68 represent the least rejected hypotheses of relationships among the species of each genus.

Figure 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. occulatus 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).

Figure 66 summarizes the least rejected hypothesis of relationship among fossil and Recent Lepisosteus. The only derived character which 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 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 boney 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.

Figure 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.

Figure 68 summarizes the relationship of fossil and Recent *Atractosteus*. *Atractosteus strausi* is considered *Atractosteus incertae sedis*, and its inclusion in the genus is based on reduction of enameloid on the infraorbitals. *Atractosteus tropicus* is hypothesized 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 which is 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 below 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) use of the term "*incertae sedis*"; and that of Patterson's and Rosen's (in press) use of the term "plesion." Nelson (1972a) suggested that the term *incertae sedis* be reserved for fossil species or fossil groups of uncertain relationship. These *incertae sedis* species or groups of species are listed below at the level that their preserved characters allow their phylogenetic placement. Patterson and Rosen (in press) feel the advantage of Nelson's use of the term is that it separates the uncertainties about the placement of Recent groups brought about because of deficient theories of relationship from the uncertainties about the 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 nonmonophyletic 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 which 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 which it is a part of, and, the plesion does not affect the hierarchical position of recent groups with which it is associated. Thus, if later information is gathered concerning the relationships of the plesion, then its position in the classification can be changed without affecting the formal hierarchical 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 <u>incertae sedis</u>, (2) fossil species or groups of species can be incorporated into a classification of Recent organism 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 affecting 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 Teleosti
  - 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*. *occidentalis* *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 figures 69-72 and are discussed below.

Distributional patterns of the genera. Figure 69 shows the distributional patterns of *Lepisosteus* and *Atractosteus* projected on a map of present continental positions. The *Lepisosteus* generalized track includes the ranges of a 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. These species-group tracks will be examined in a separate section below.

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 Carribbean species (A. tristoechus), one African species (A. africanus), and one European species (A. strausi). Like the Lepisosteus generalized track, the Atractosteus generalized track 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: (1) both genera are found on parts of what were once Laurasian and Gondwanian land masses; (2) the genera show a large amount of sympatry, both in 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; and this dispersal may have occurred over a Pangean landscape rather than a landscape of present continental positions; (3) because an allopatric speciation event (a vicariance event) must come before a dispersal which produced sympatry, the vicariance event which produced the two genera may have occurred before the break-up of Pangea. Thus, the minimum age of the genera of gars is hypothesized here as 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 American European, or Indian forms. Whether the western ranges of the primitive members of the genus represents 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, or 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 which describes the range of the group made up of *L. platostomus* and more derived species is identical with that which describes 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 (Cret.). This track is hypothesized 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. platyrhincus*, 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 which split the common ancestor of *L. fimbriatus* and *oculatus* - *platyrhincus* is hypothesized to be Early Eocene in age.

Atractosteus species group distributional patterns and Rosen's hypothesis of Carribbean biogeography. Rosen (in press) has reviewed the biotic composition of the Carribbean region and concluded that several generalized tracks composed of many diverse organisms were involved in producing the distributional patterns which appear in the region today. Two of these generalized tracks involve species of the *A. spatula* species group and will be discussed here. They are (1) the North American-Carribbean generalized track and (2) the Carribbean-West African generalized track.

The *A. spatula* species group form a track (fig. 71) composed of species from North America, nuclear Middle America, Africa, and the Carribbean. Within this track is another track (fig. 72) composed of the two disjunct populations of *A. spatula* and the Carribbean *A. tristoechus*. Rosen (in press) concluded that the Recent *Atractosteus* distributions in the Carribbean region were probably a part of an older North American-Carribbean generalized track of Pangean or Laurasian affinities as opposed to a younger

North-American-Carribbean track with primarily Gondwanian affinities (a component of which would be *Gambusia*, for example). Further, Rosen concluded that the final determination of phylogenetic affinities among Recent *Atractosteus* would help determine the relative age of the vicariance event which 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 Carribbean Region at a time when (following Rosen's conclusions concerning the origin of the Carribbean), the Carribbean region would still be part of the Pacific seafloor. The minimum age of this track can be estimated from the current estimate of the 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-Carribbean track discussed by Rosen (in press) and is not necessarily older than similar distributions which conform 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 heirarchy 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 which produced the *indicus-osseus* species pair is older than the event which 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 which is a component of a younger North American-Carribbean generalized track.

The model of gar biogeography presented above predicts that *Lepisosteus* gars will be found as a component of the African biota. Further, 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.

Summary

(1) The objectives of this study were four fold: (a) to determine if the lepisosteids, or gars, are a monophyletic group; (b) to determine which of the current theories of the relationships of gars to other actinopterygian groups is most highly corroborated; (c) to determine which nominal fossil and recent gar species could be recognized as valid species and what the interrelationships of these species are; (d) to describe the major features of gar biogeography.

(2) Hennig's (1966) phylogenetic method is used to study objectives a, b, and c. Hennig's method is briefly summarized and several points taken up in detail. Croizat's (1958, 1962) biogeographic method is used for objective d.

(3) Various anatomical features of gars are compared to other actinopterygian and teleostome groups. The analysis concentrates on the skull, visceral arches, pectoral girdle, and post-cranial 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 systematic section ends with a classification. The Division Ginglymodi, the family Lepisosteidae, and the two genera Lepisosteus and Atractosteus are diagnosed, and synonomies are provided. Each of the recognized species is diagnosed, described or re-described, and briefly compared to other species in its genus. Synonomies of Recent species include only name changes whereas the synonomies of fossil species include all literature citations found. Described fossil forms which can not 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 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 *insertae sedis* while *A. atrox* is the sister-species of the *spatula-tristoechus* species pair.

(8) 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 pre-date the formation of the Carribbean 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 (a) *Lepisosteus* gars will be found in the fossil fauna of Africa and (b) the vicariant sister group of gars may be found among the fossil fauna of South America.

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Table 1. Neurocranial ossifications in seven groups of actinopterygian fishes. Data from Patterson (1973).

Bone	Taxon						
	Pterleidus	gars	*Lepidotes*	parasemionotids	*Amia*	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	X	X
Pterotic	X	X	X	X		X	X
Prootic	X	X	X	X	X	X	X
Basisphenoid	X		X	X	X	X	X
Sphenotic	X	X	X	X	X	X	X
Orbitosphenoid	X	X	X	?	X	X	X

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

* lowest ratio - highest ratio (mean, standard deviation)

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

* lowest ratio - highest ratio (mean, standard deviation)

Table 2. Ranges of various meristic counts for seven species of gars. Some data from Suttkus (1963).

Character	Species						
	L. platostomus	L. osseus	L. oculatus	L. platyrhincus	A. tropicus	A. spatula	A. tristoechus
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		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

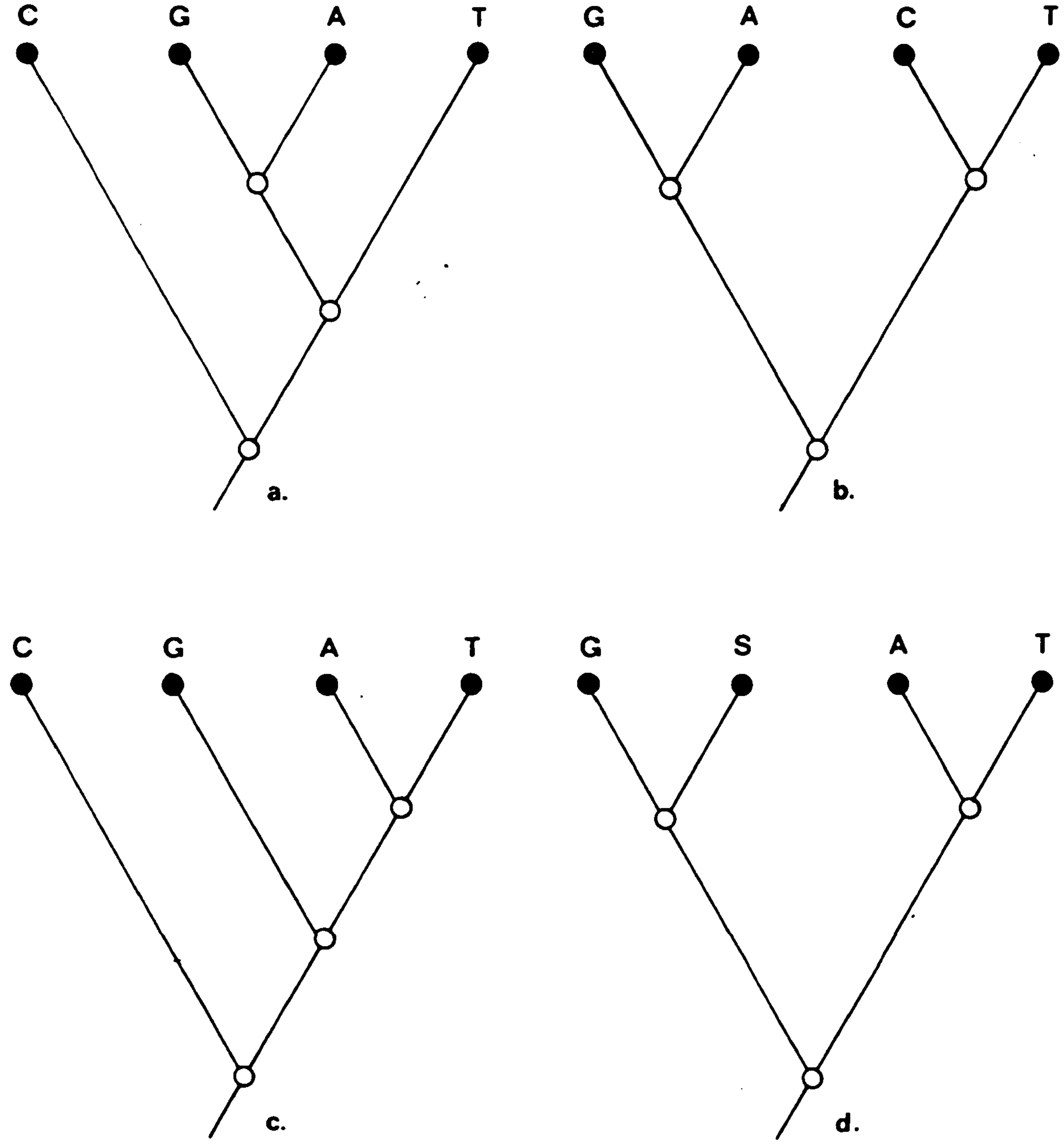

FIGURE 1

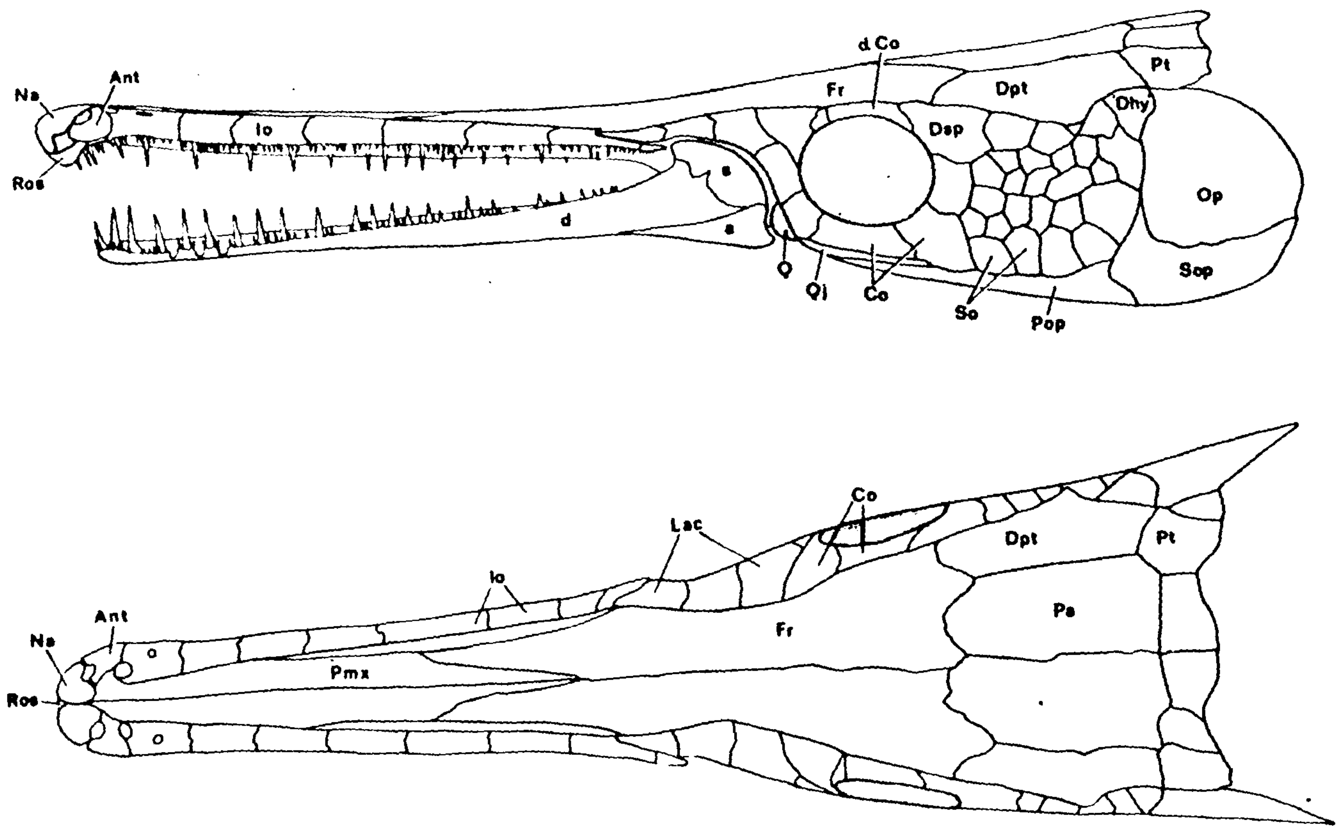
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FIGURE 2

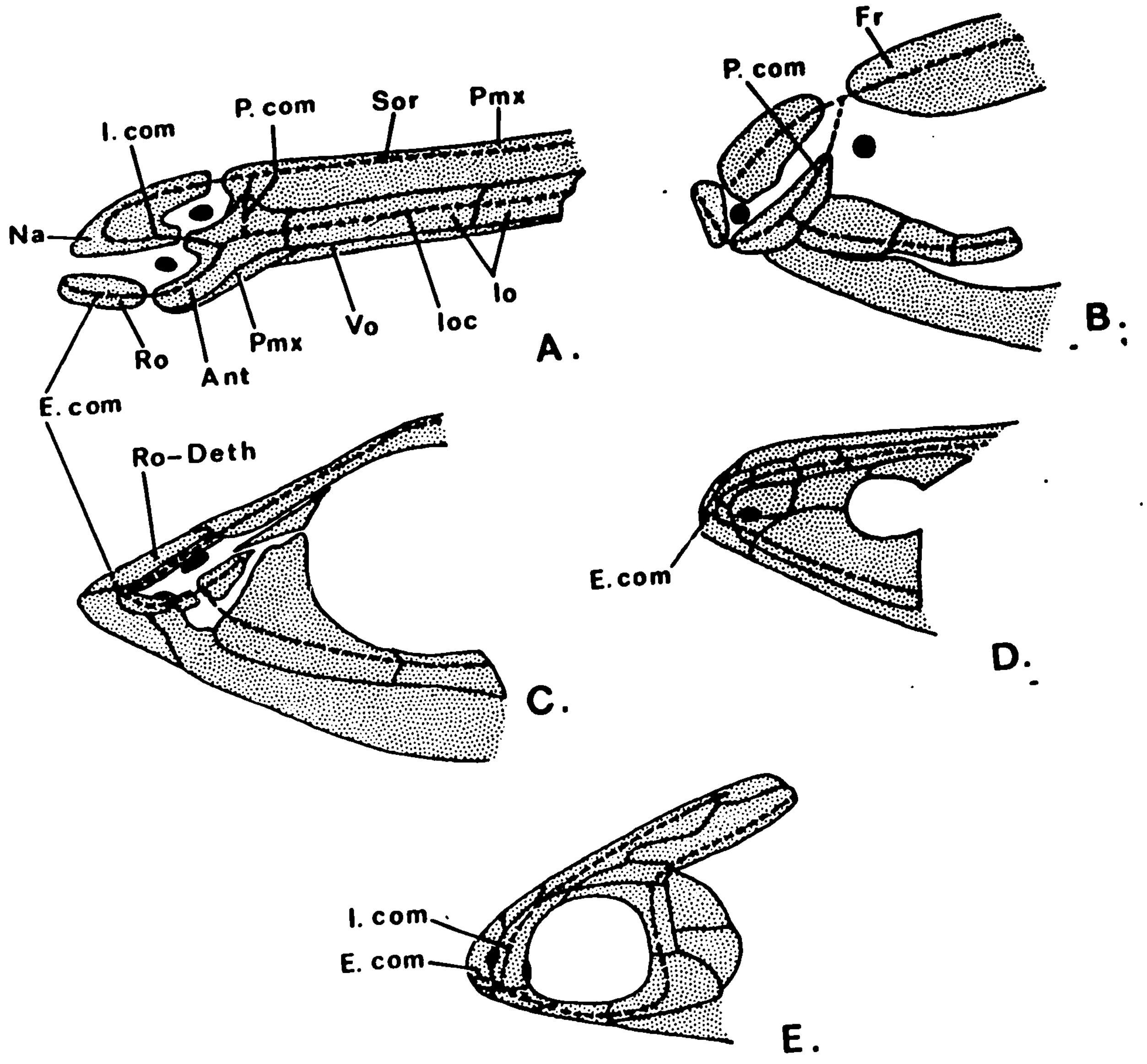
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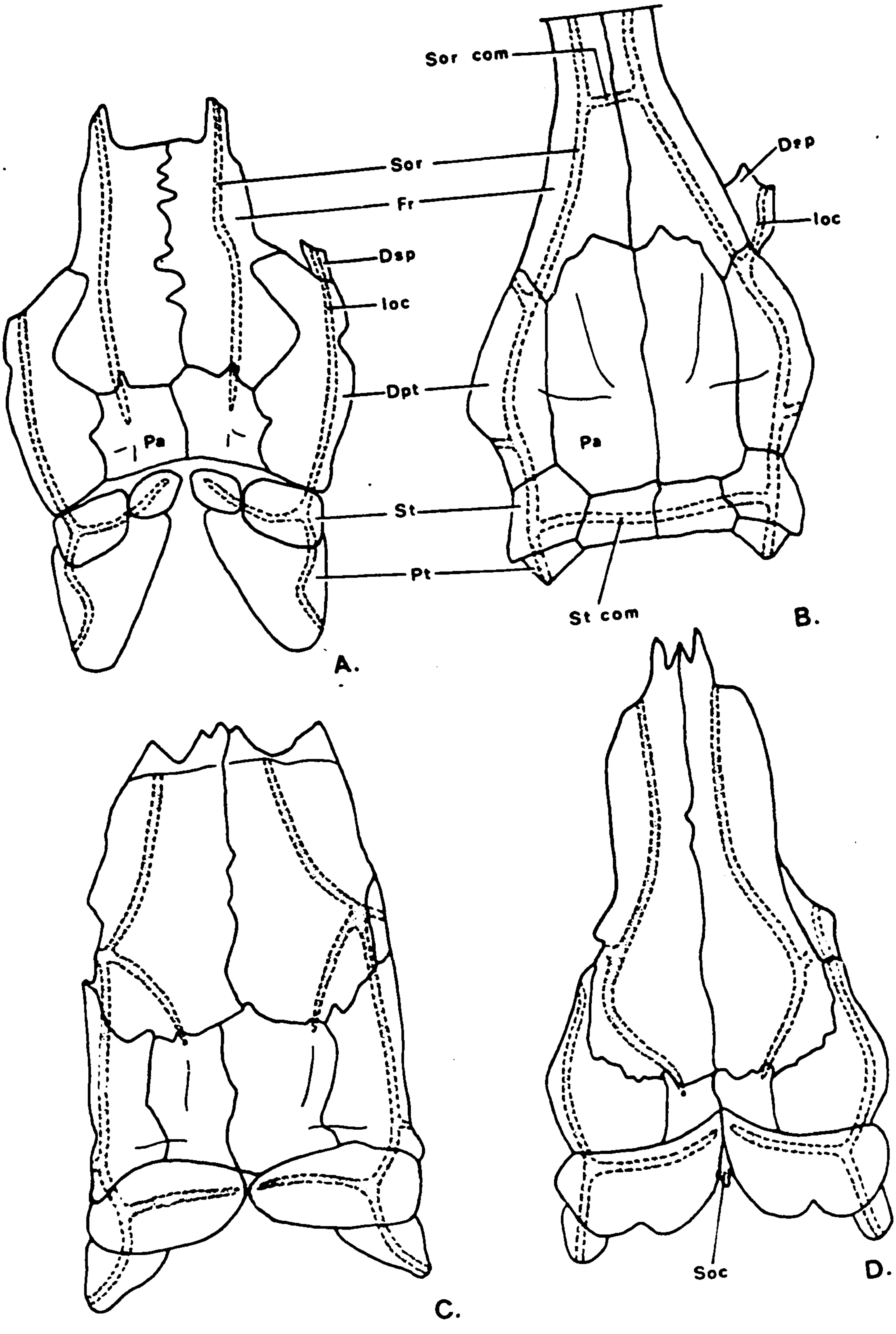
FIGURE 3



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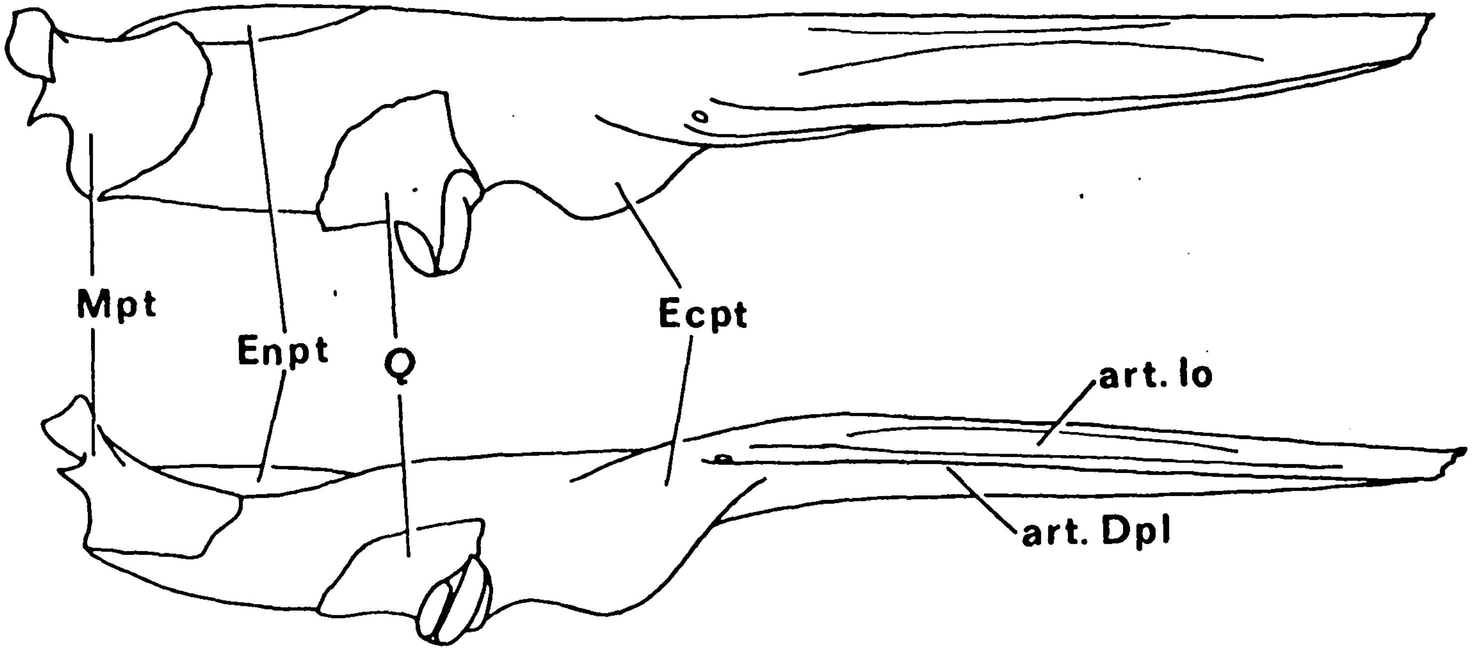
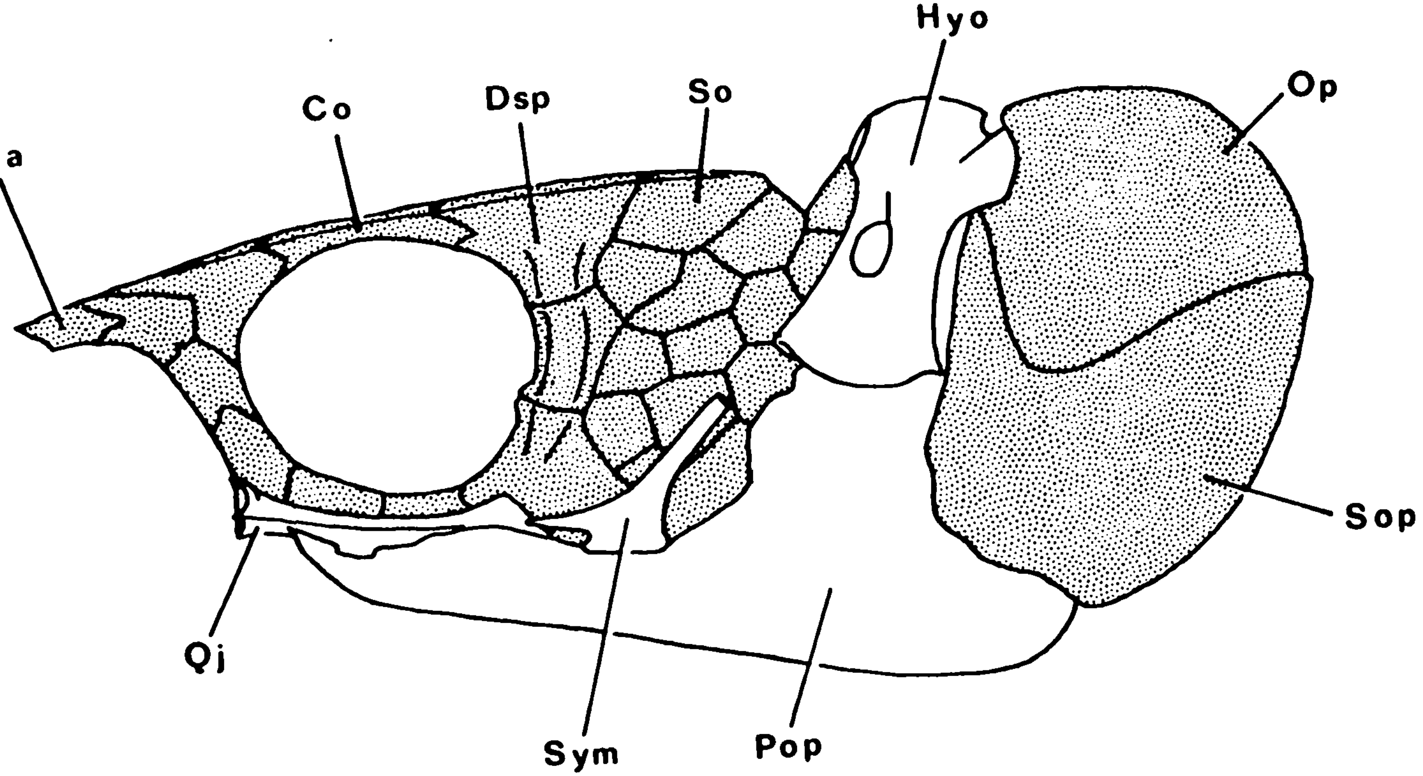


FIGURE 5



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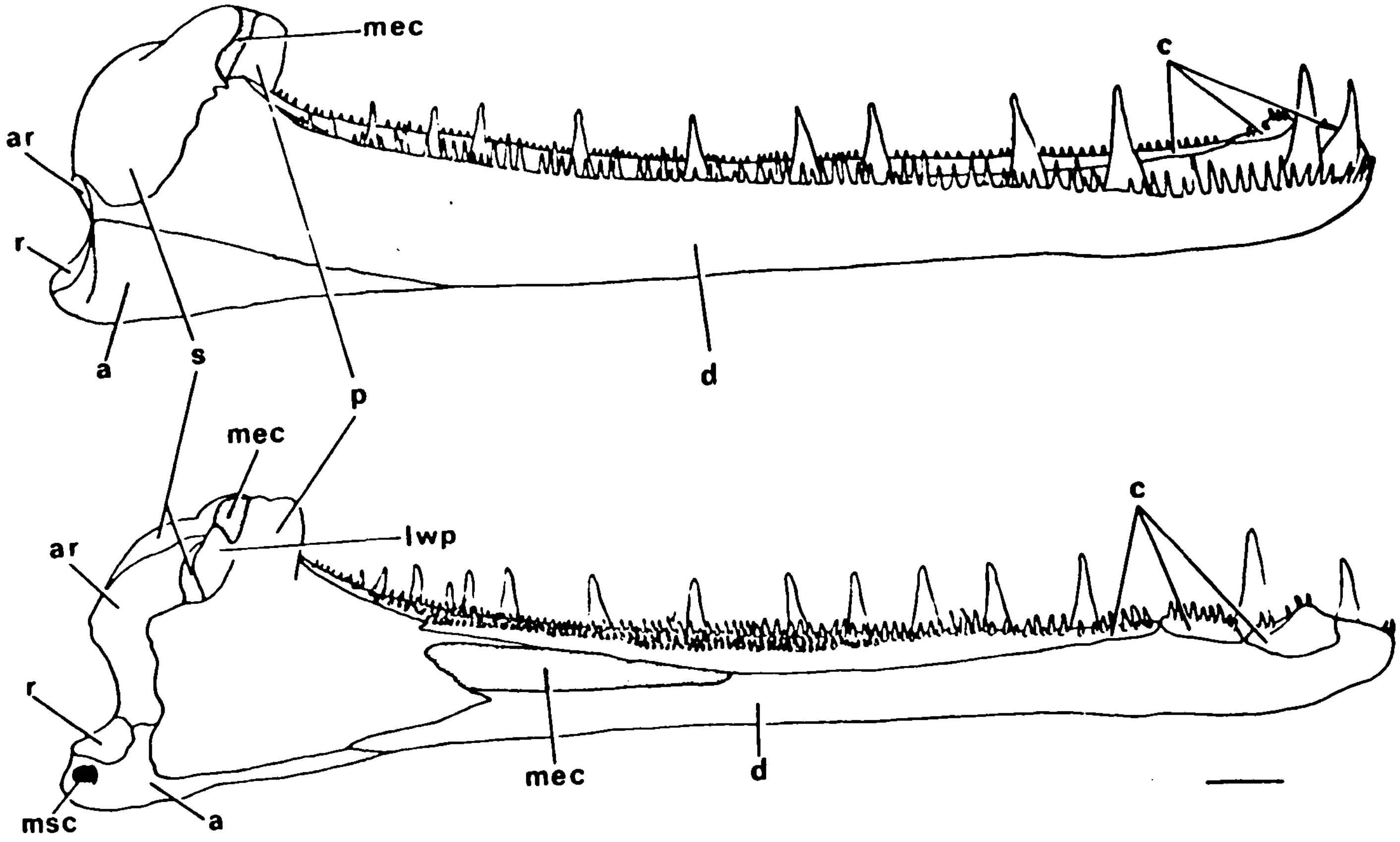

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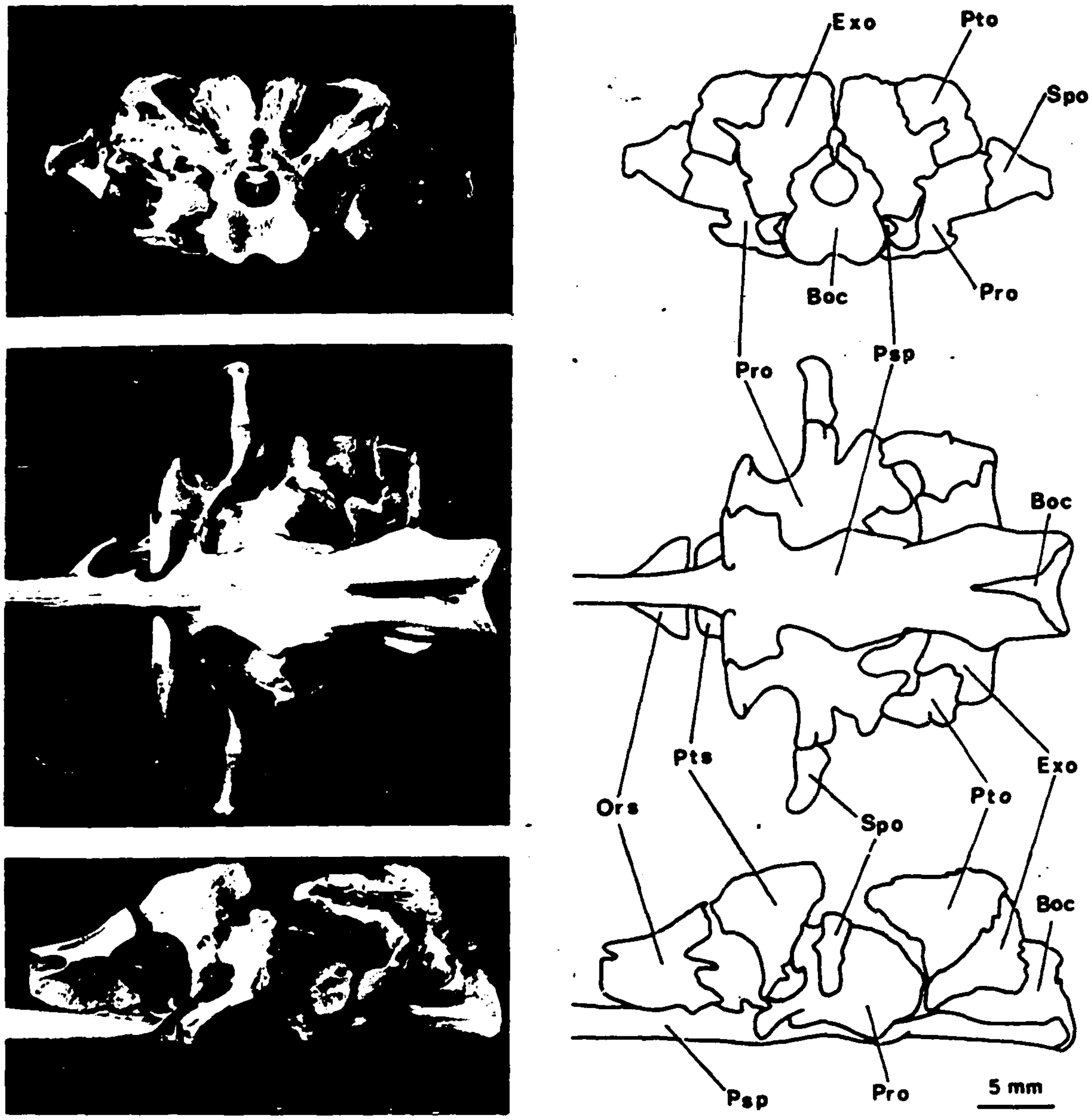
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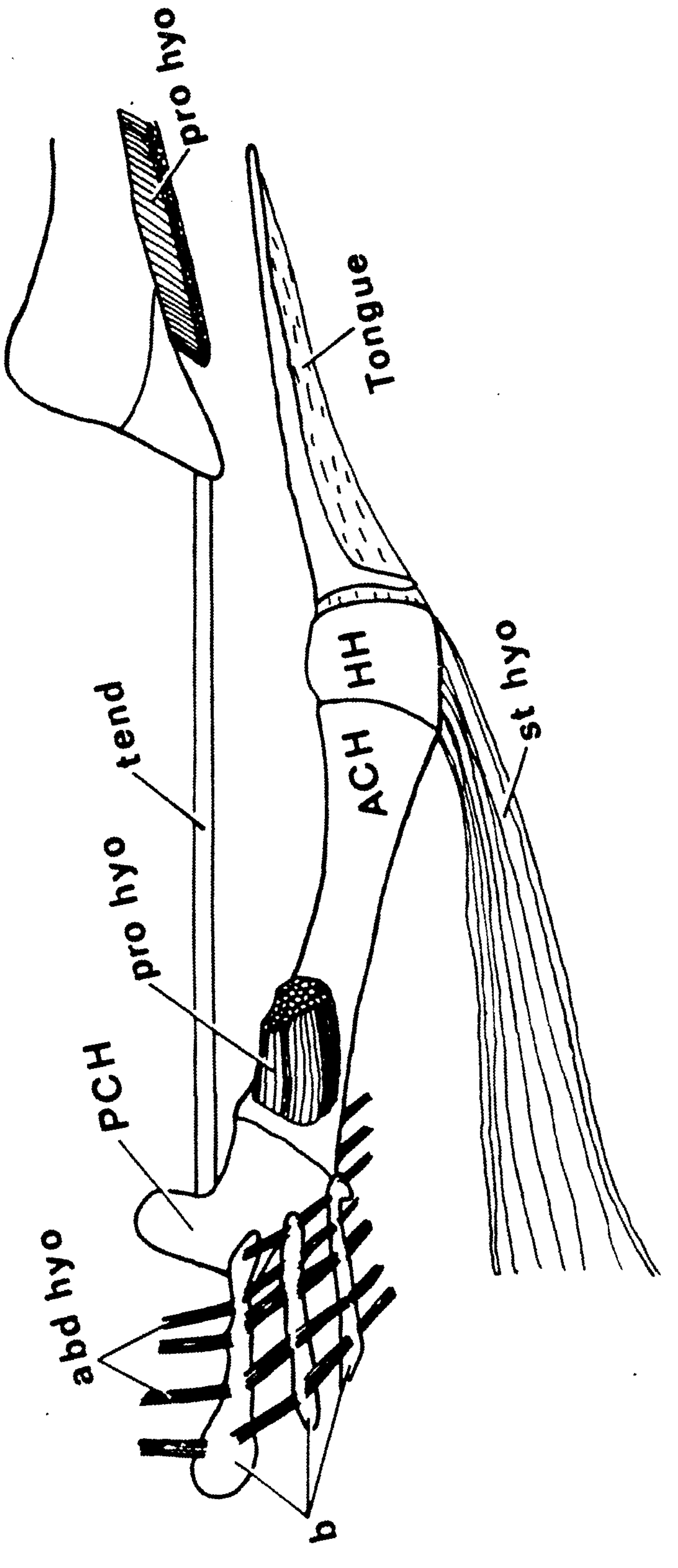
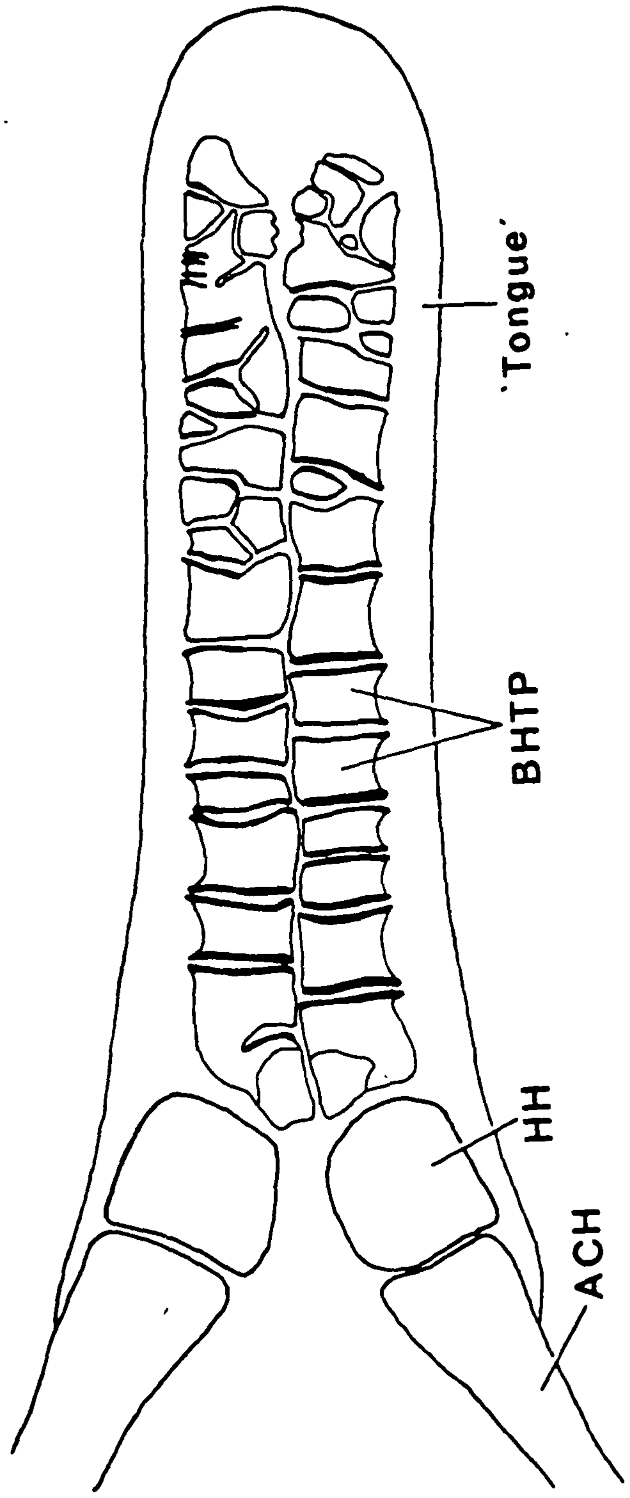


FIGURE. 9



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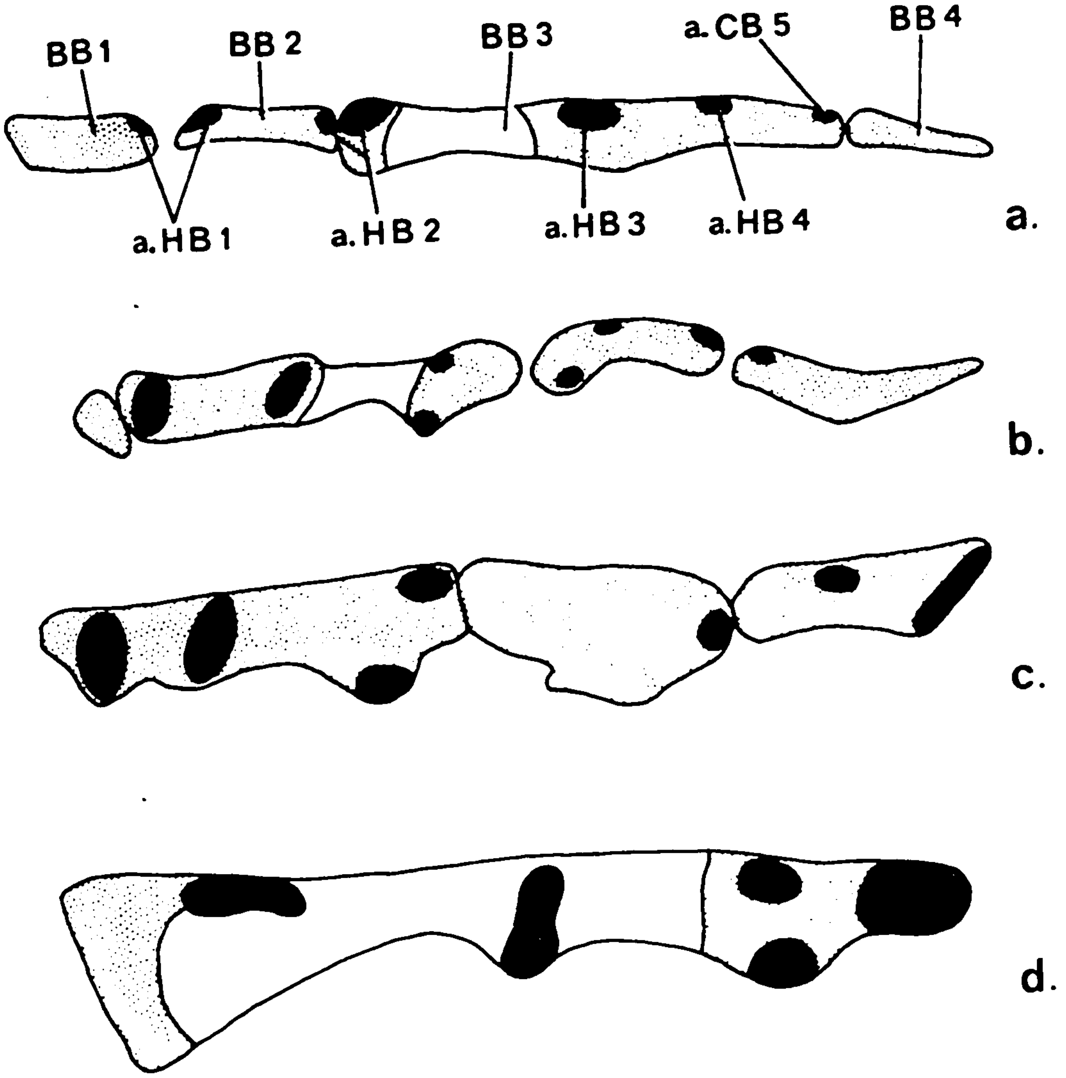

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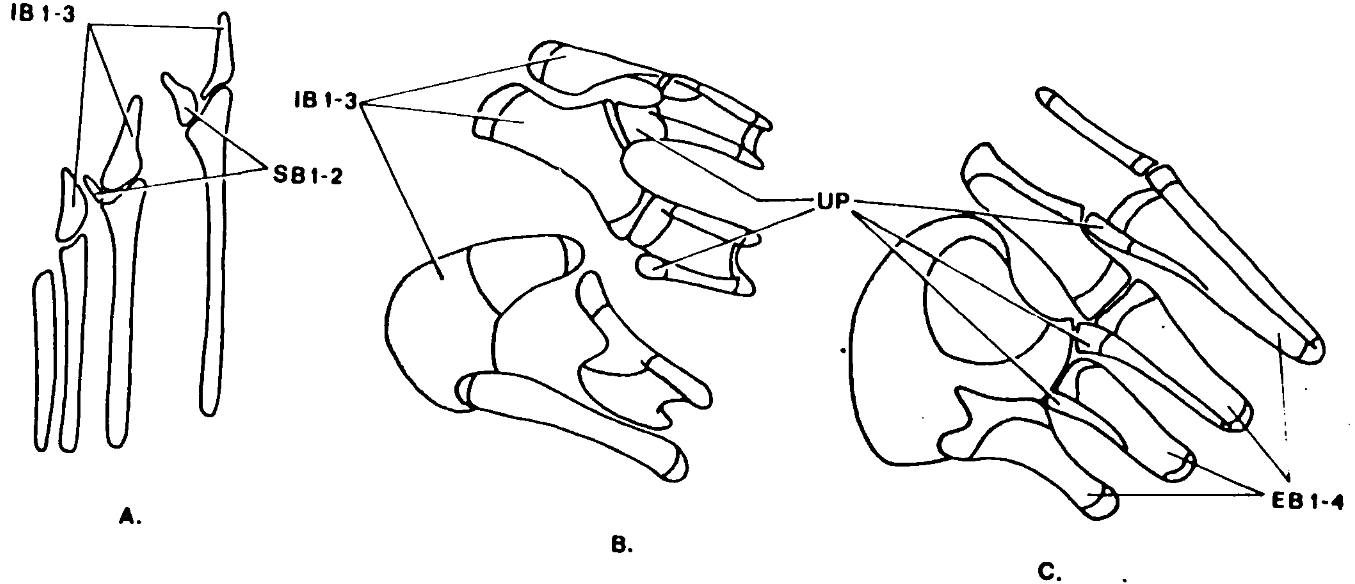

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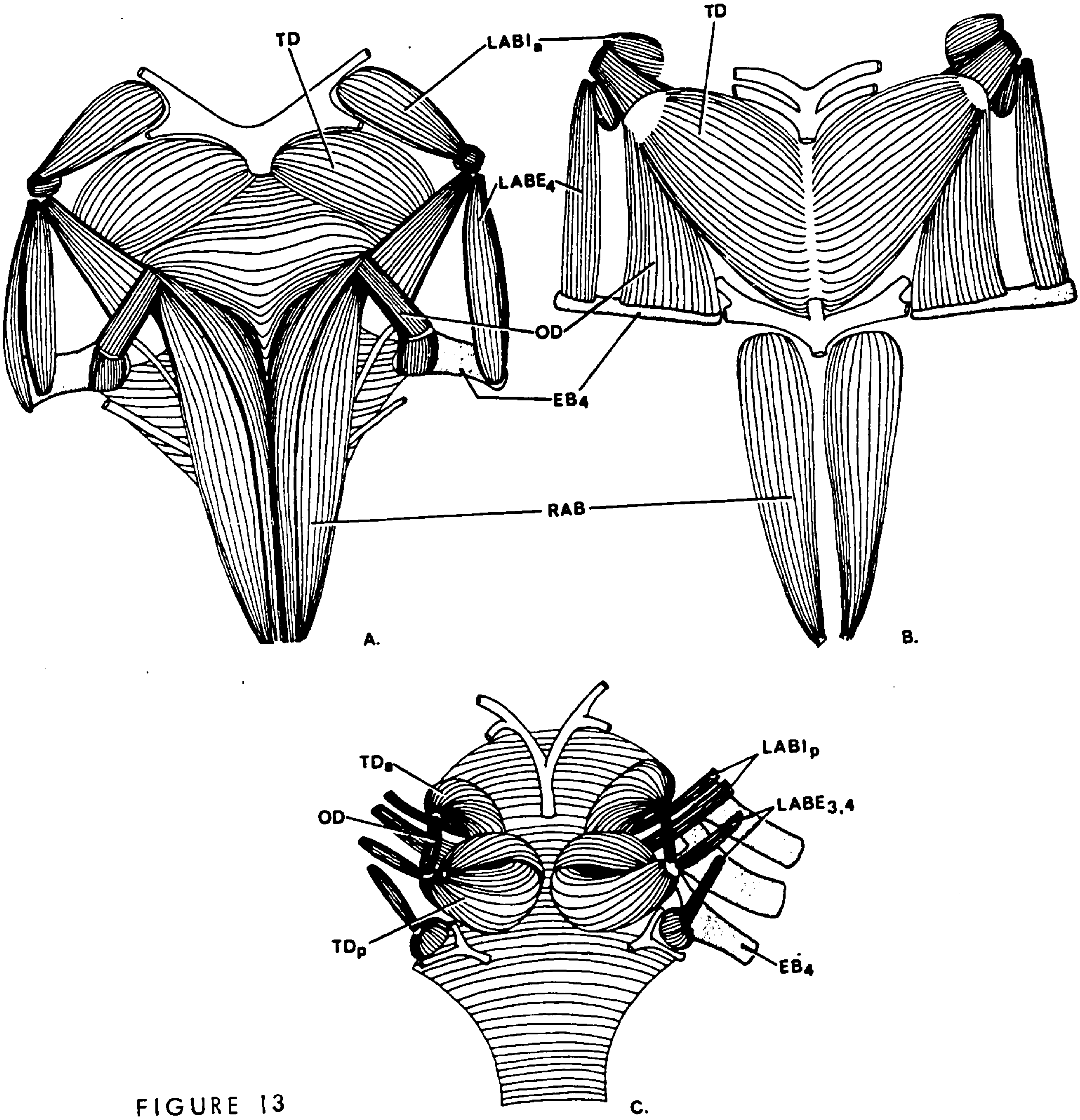

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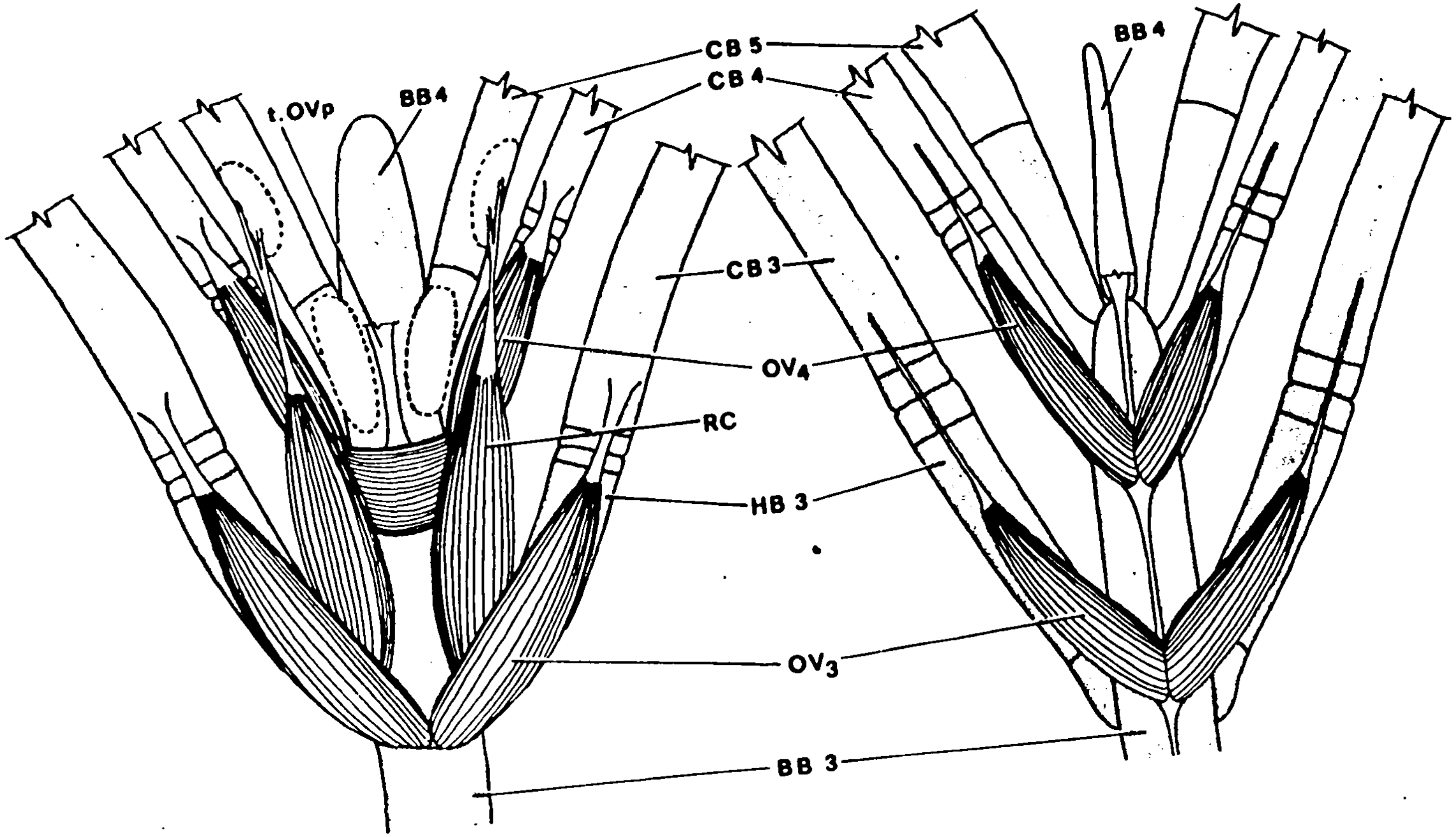

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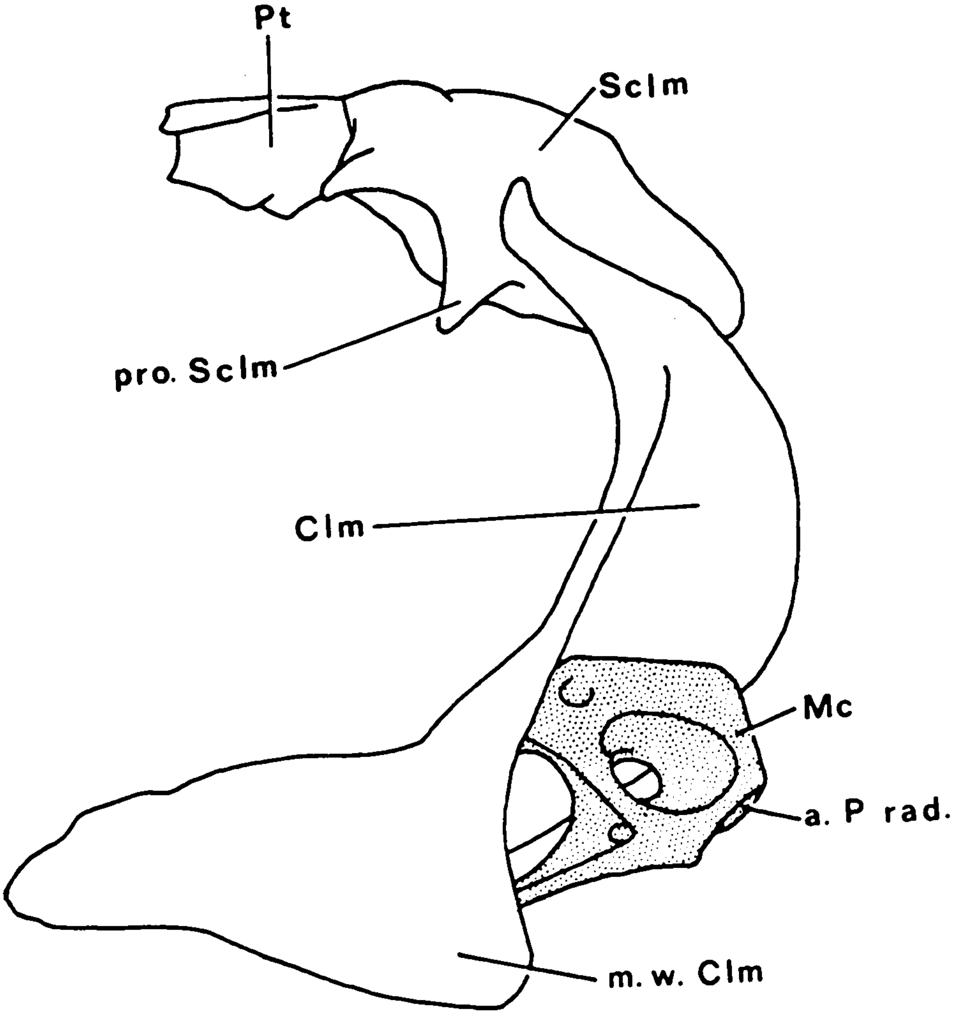

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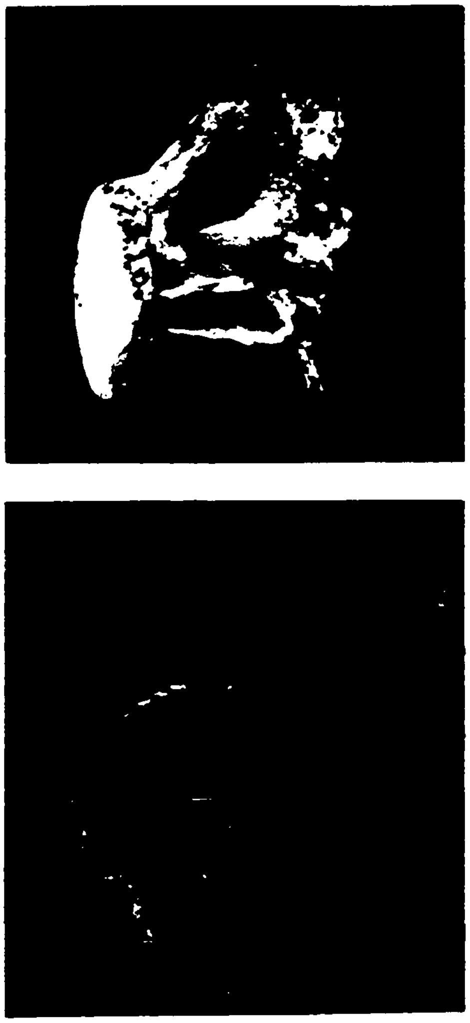


FIGURE 16

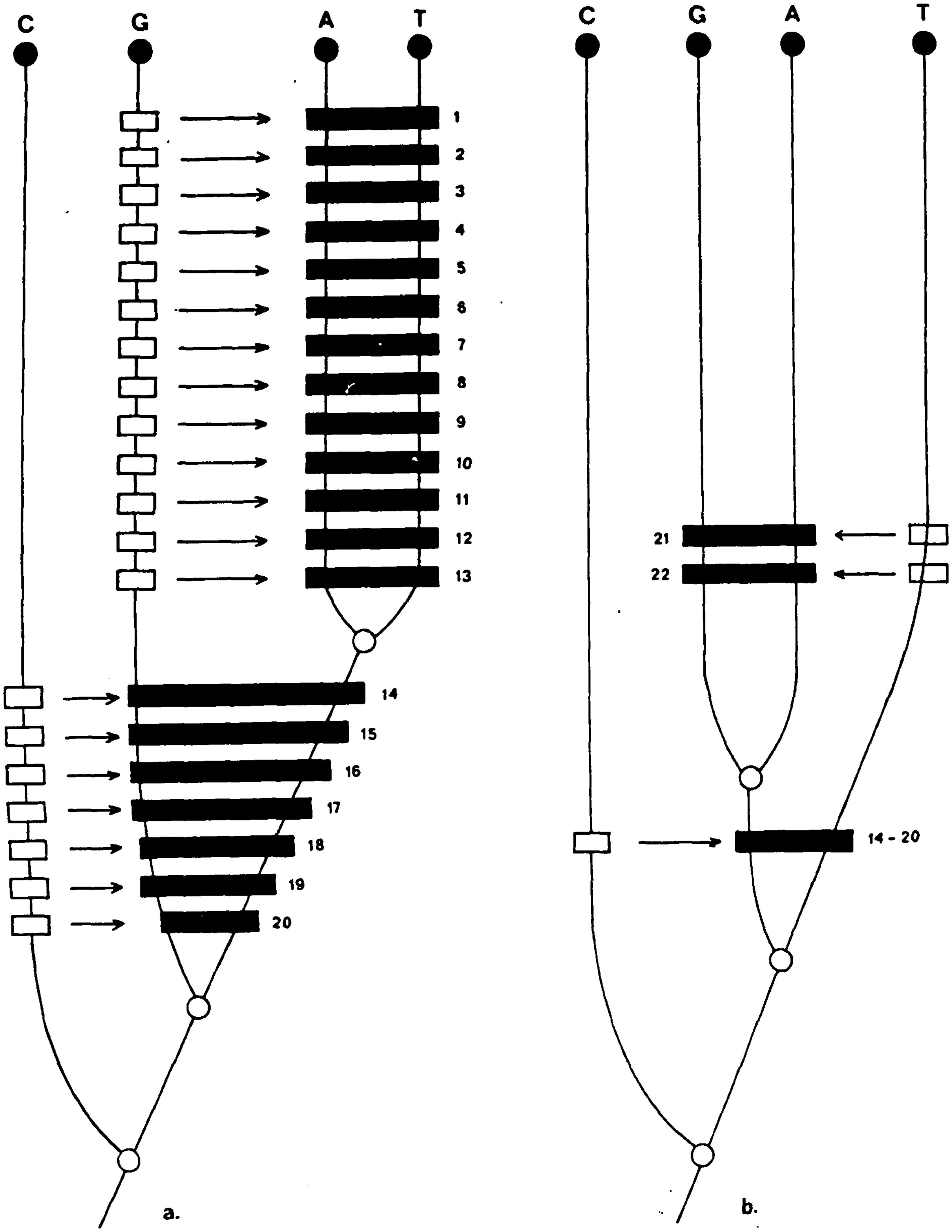
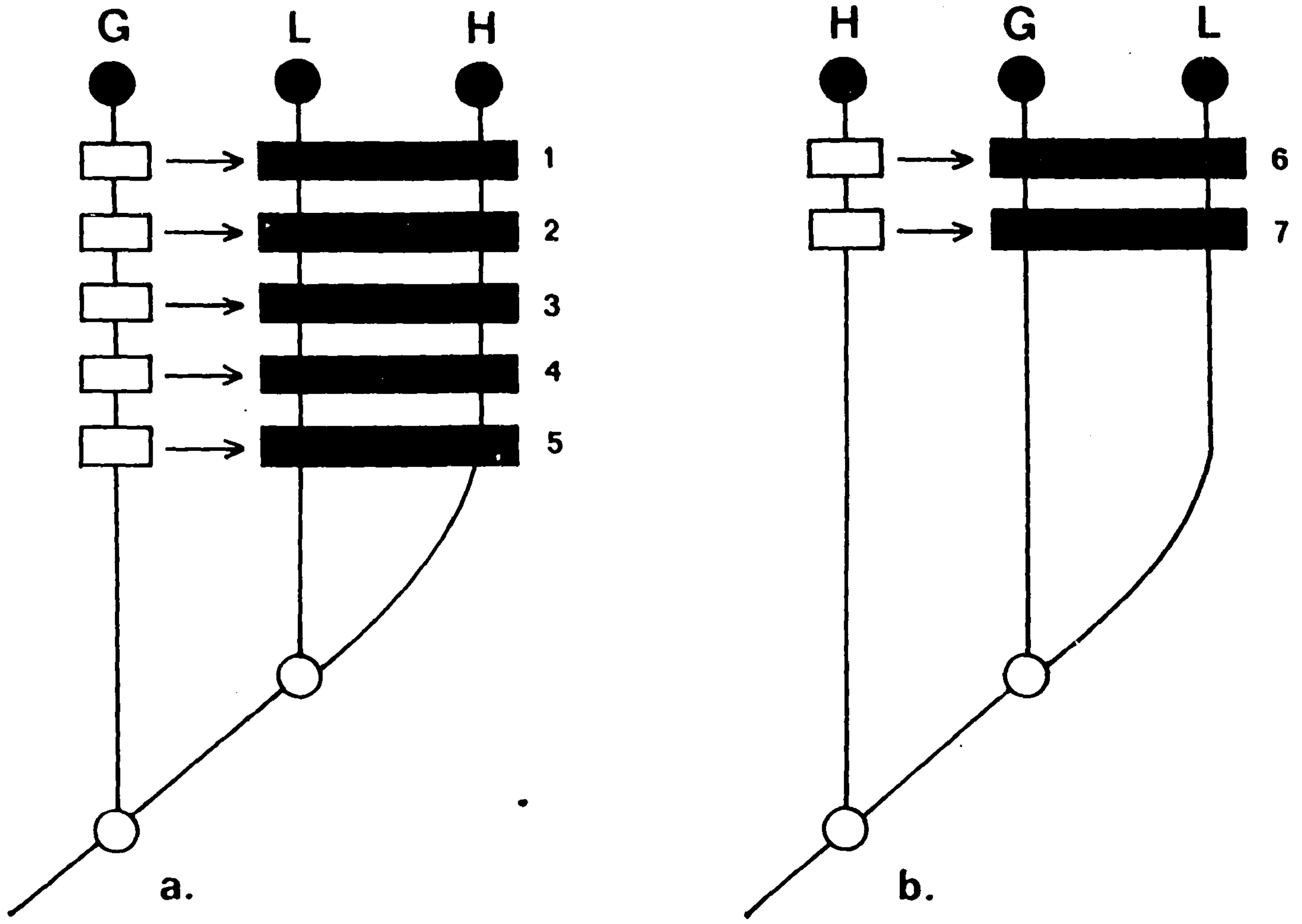


FIGURE 17



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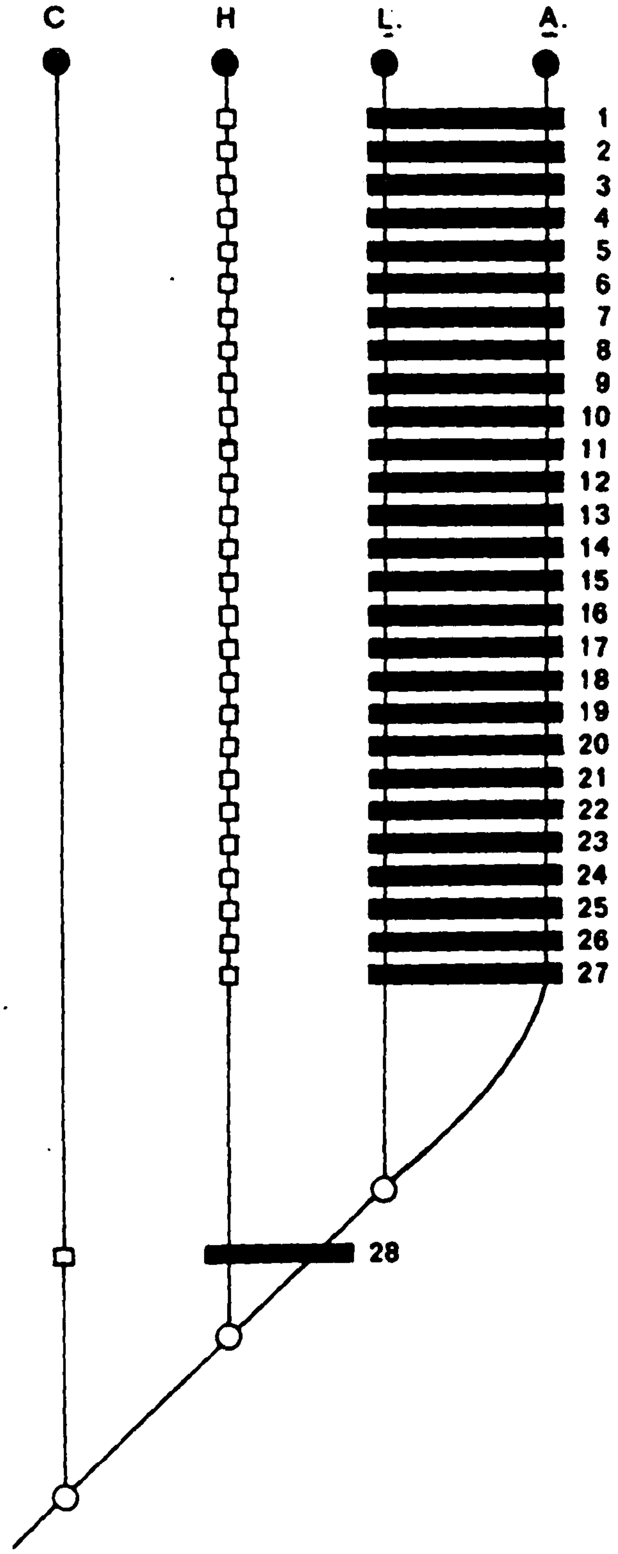
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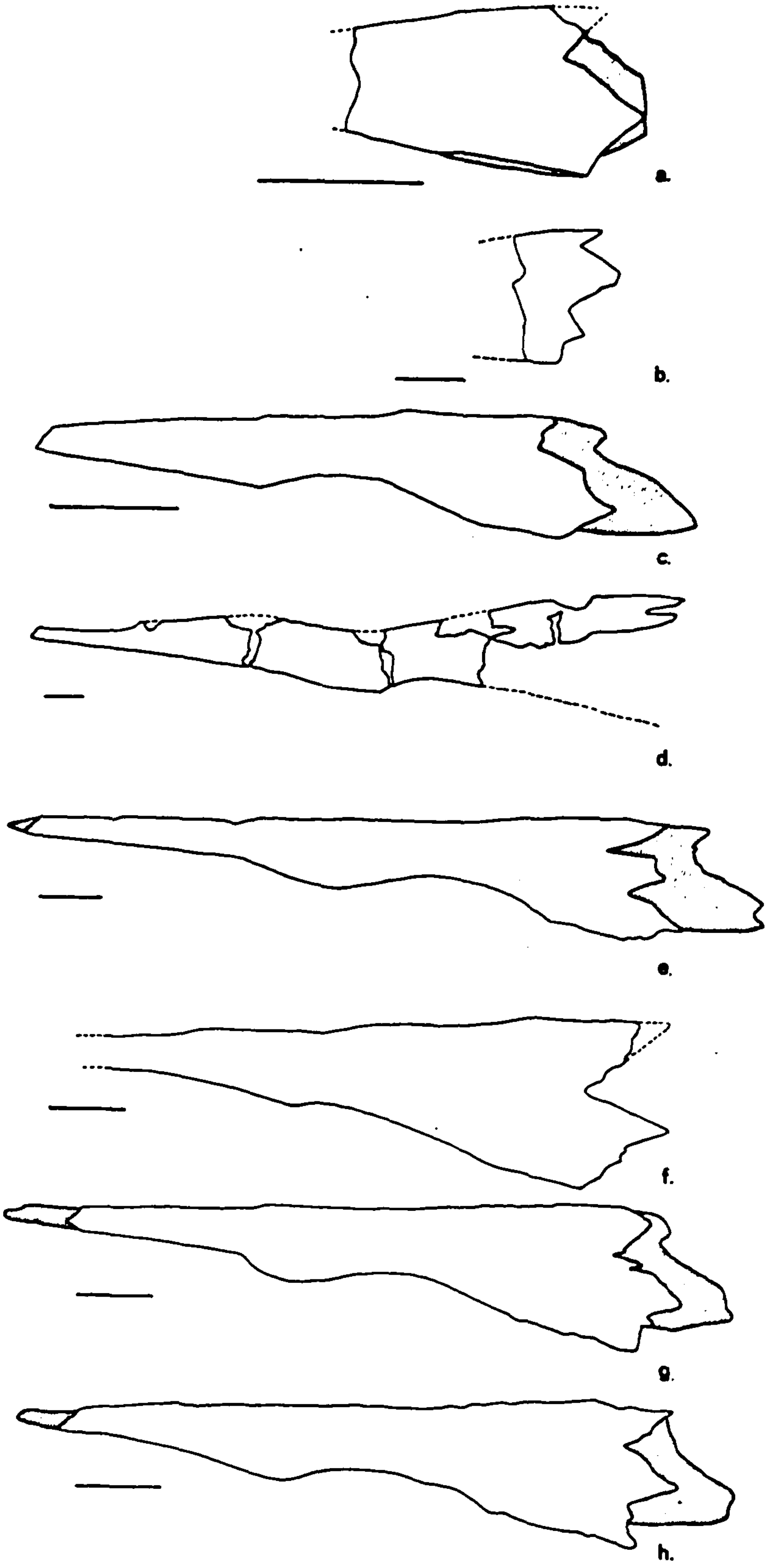
FIGURE 19



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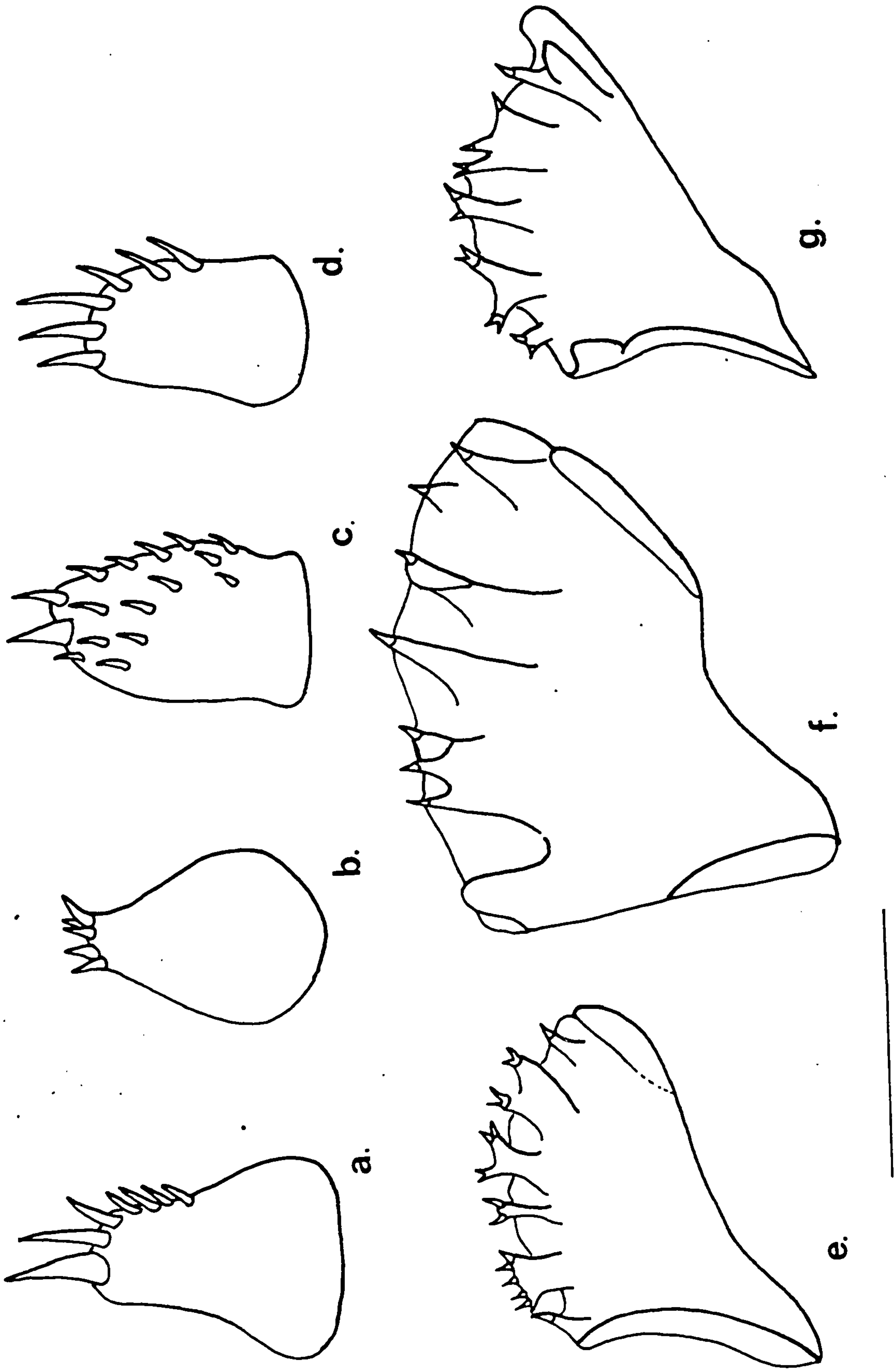


FIGURE 21

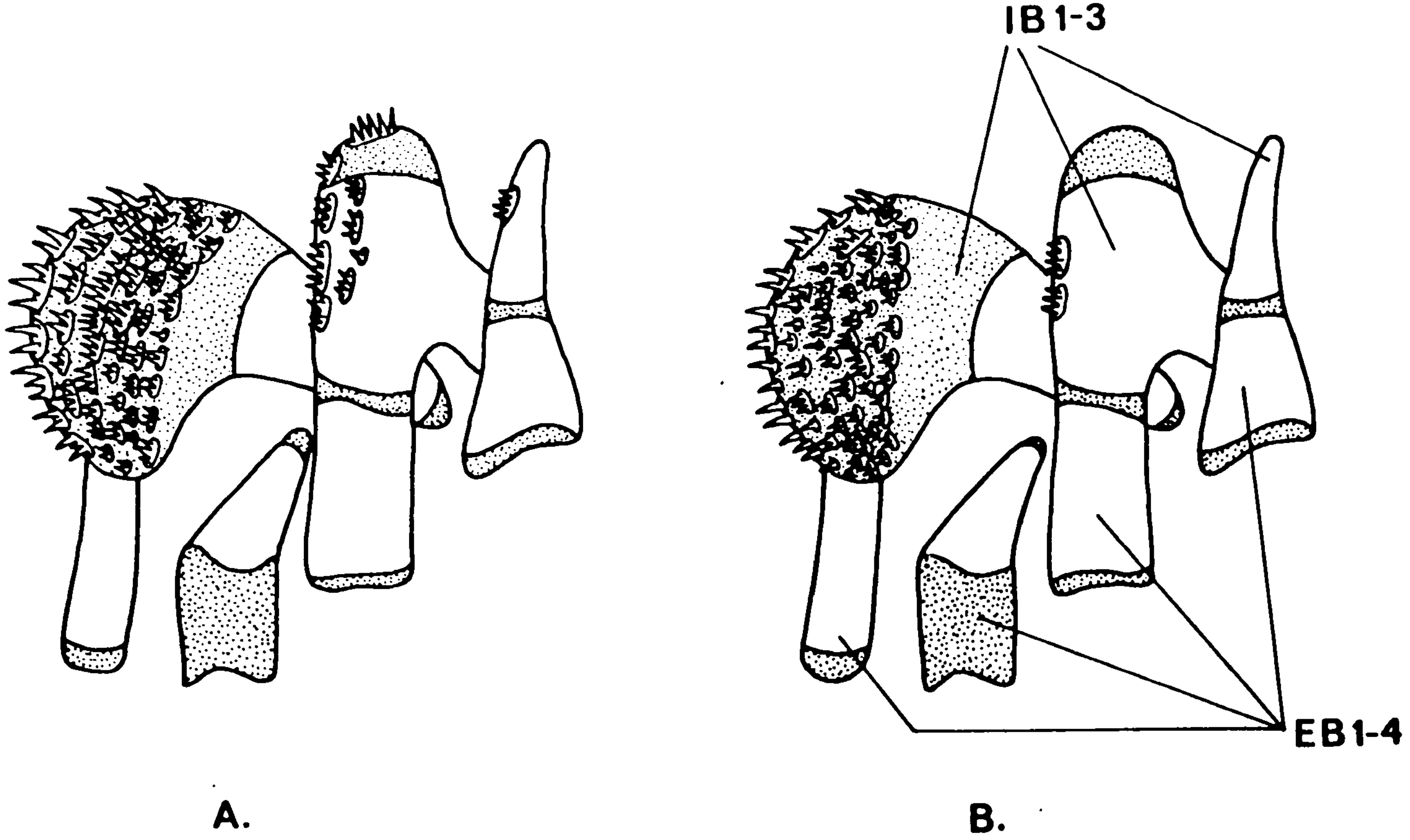
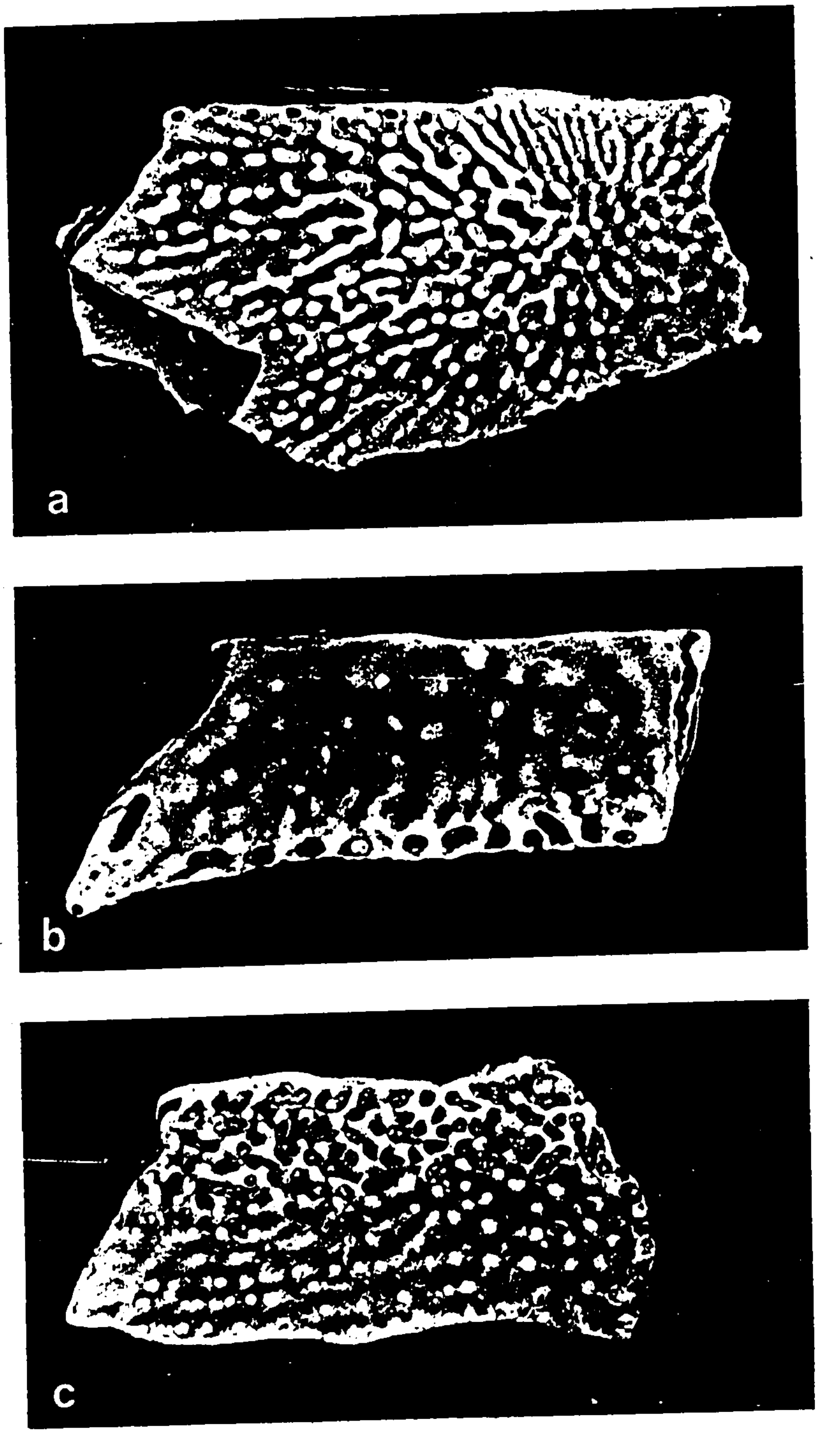


FIGURE 22



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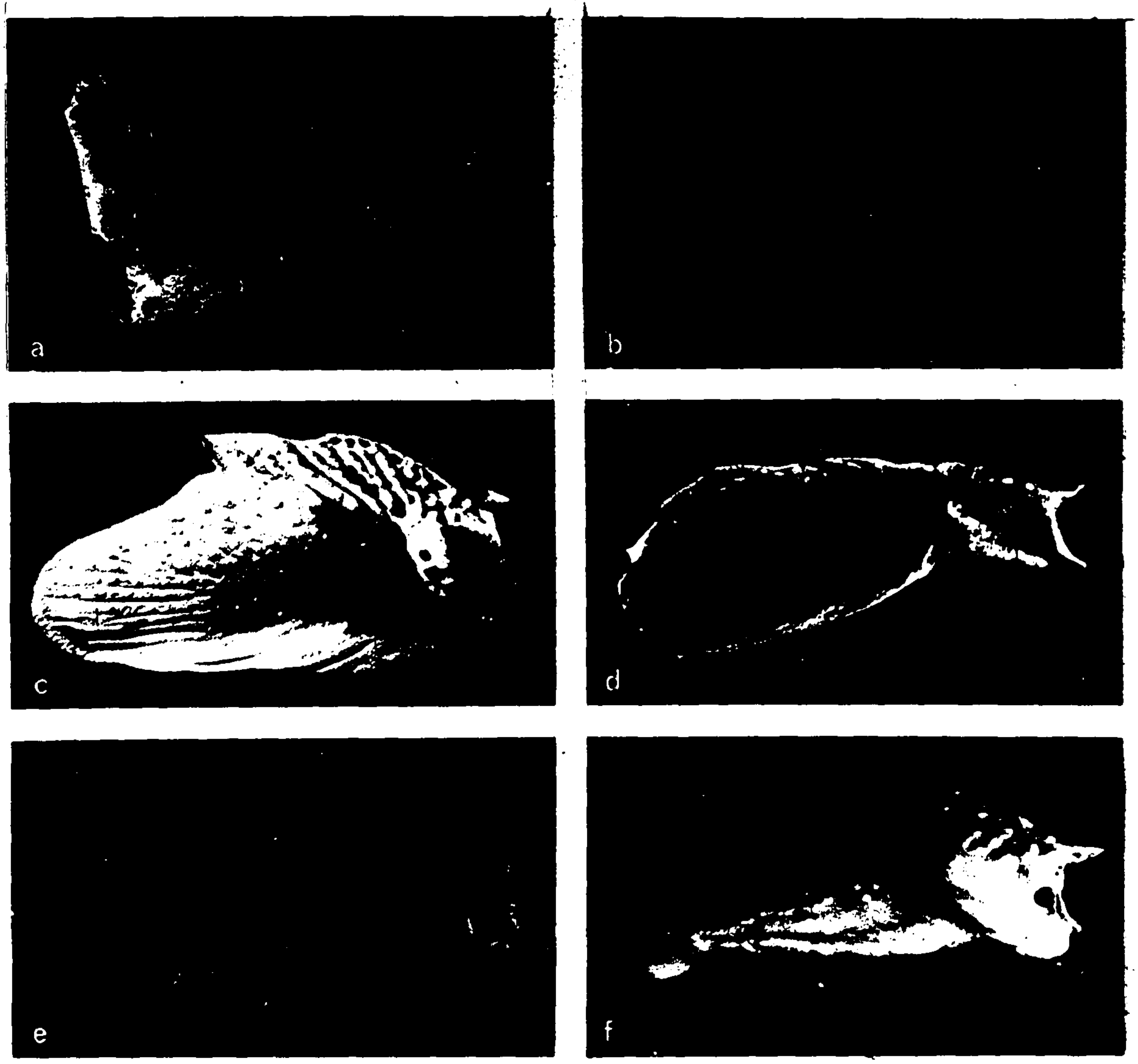

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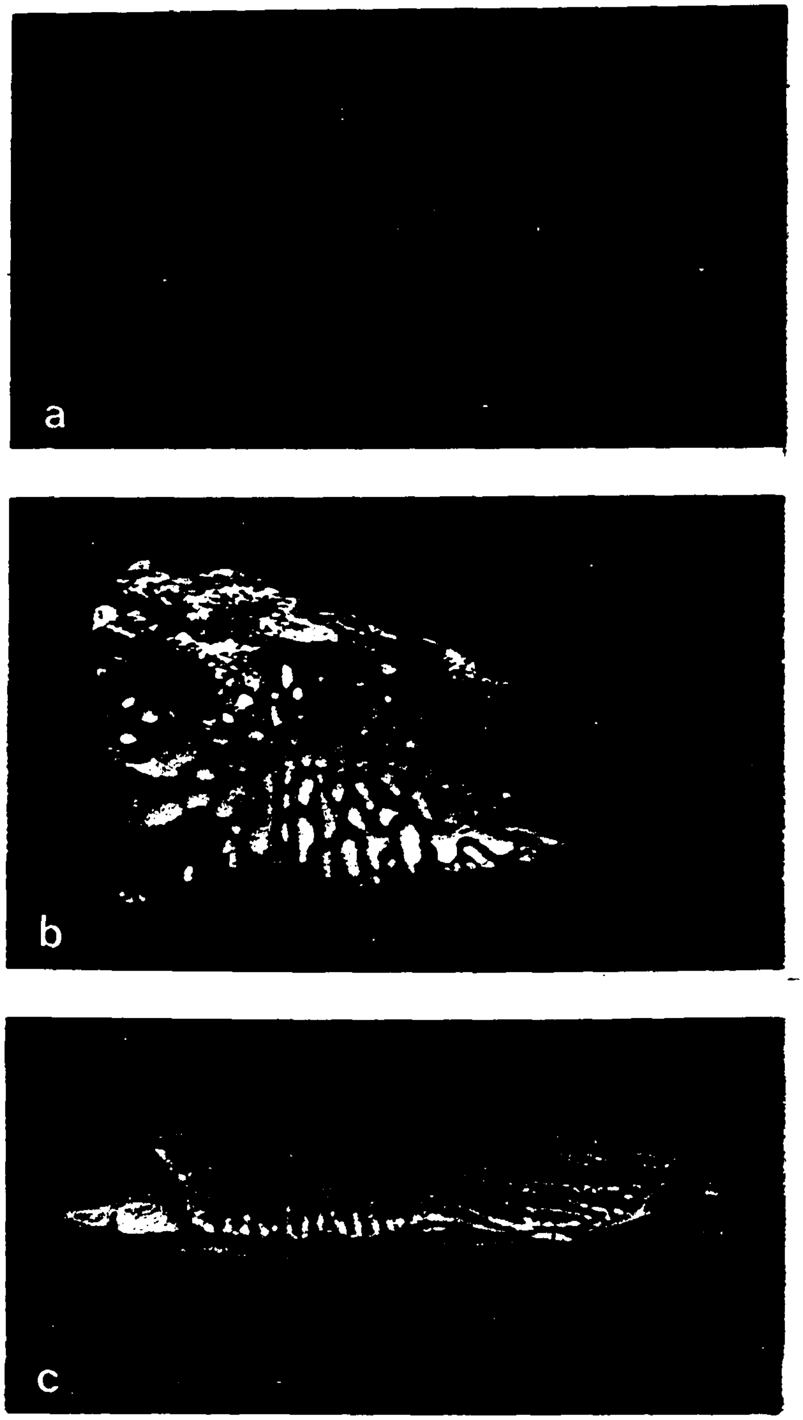

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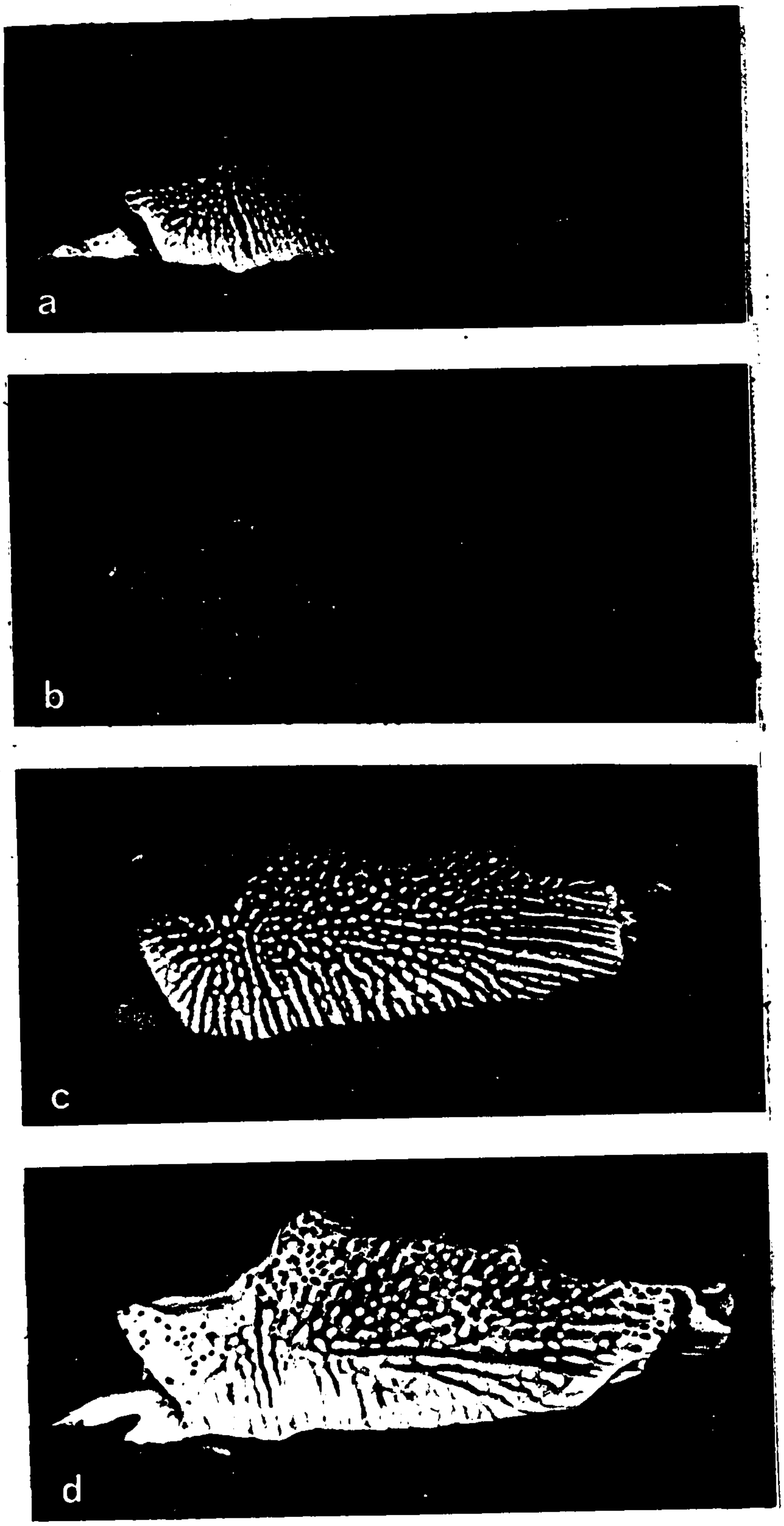

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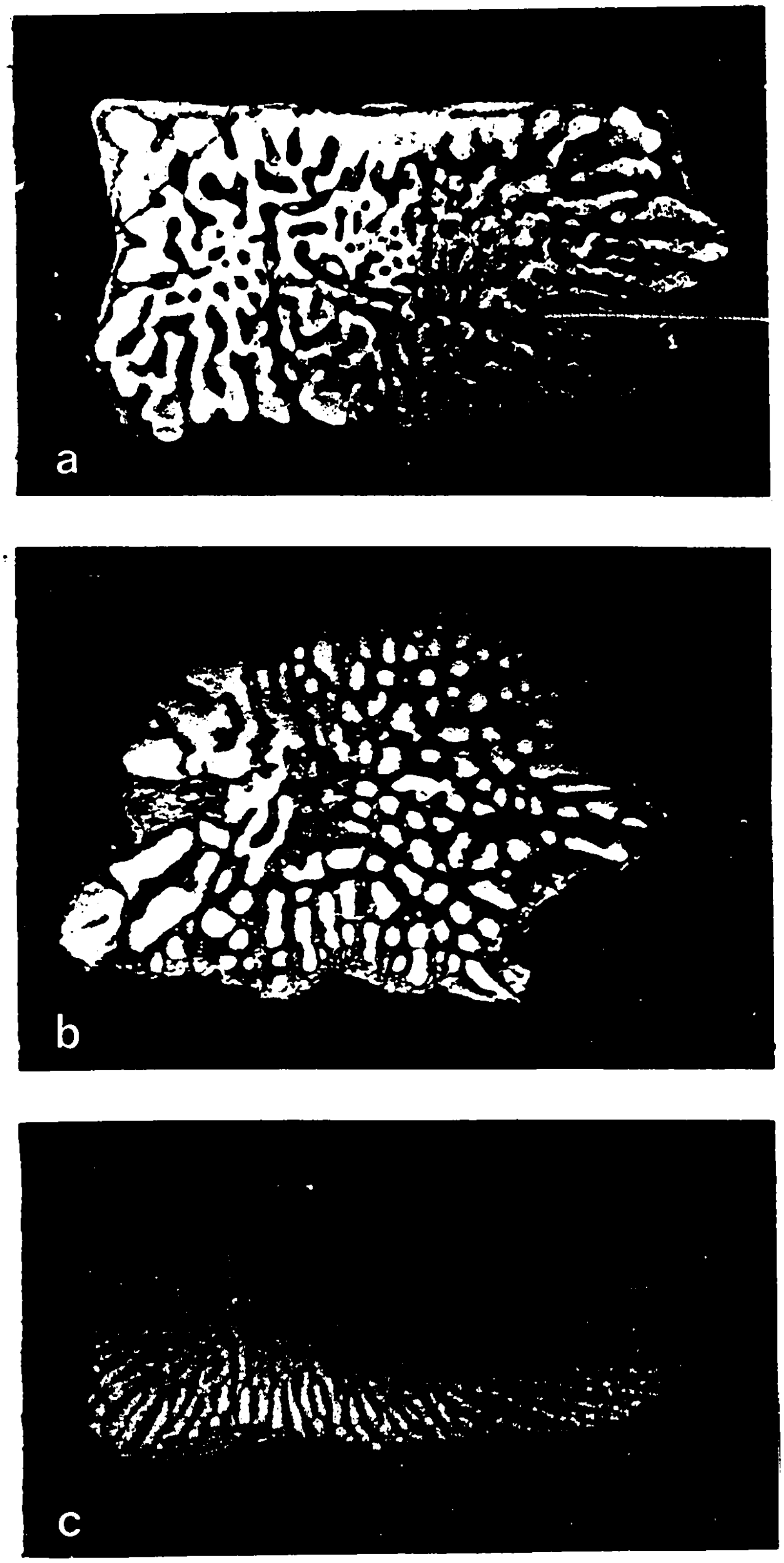

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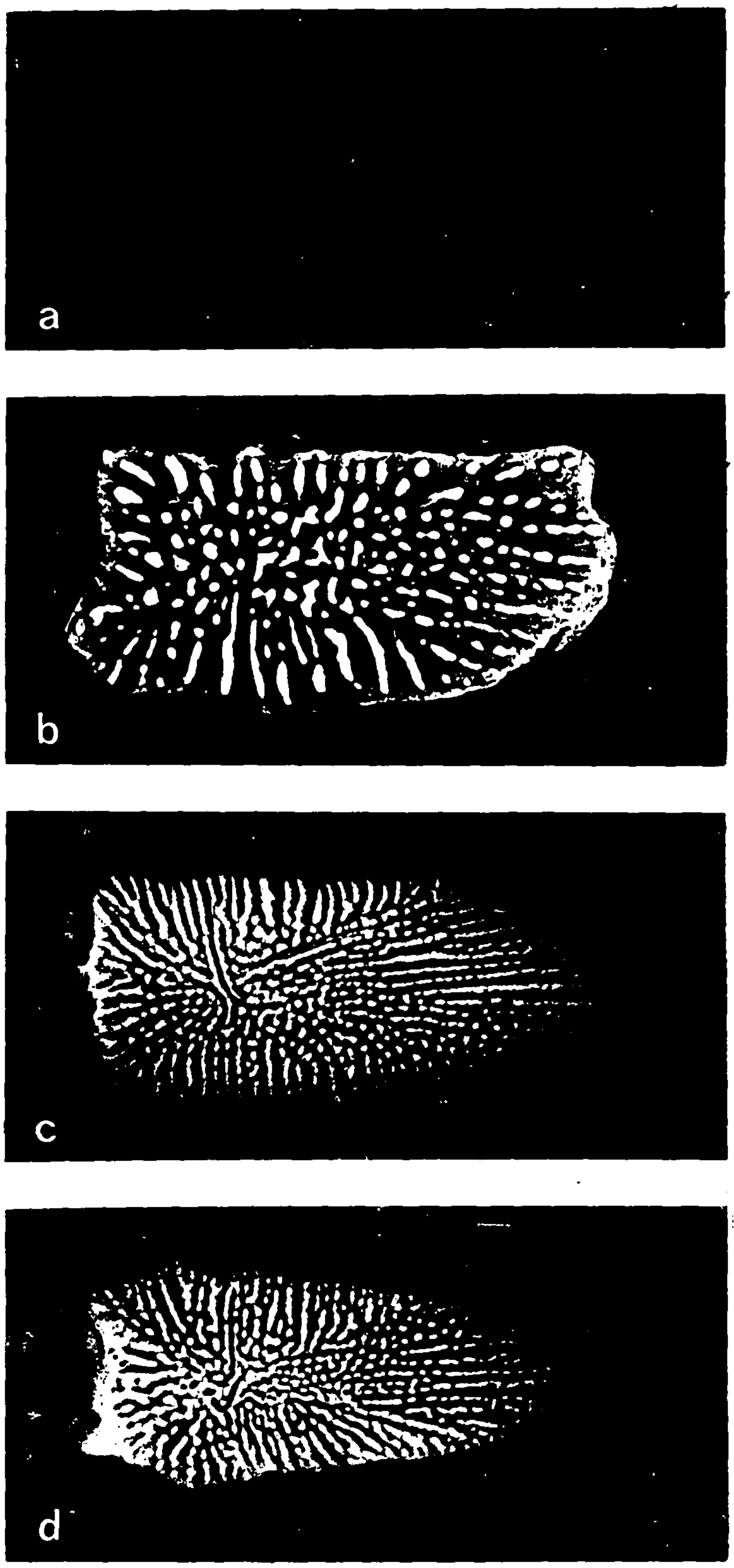

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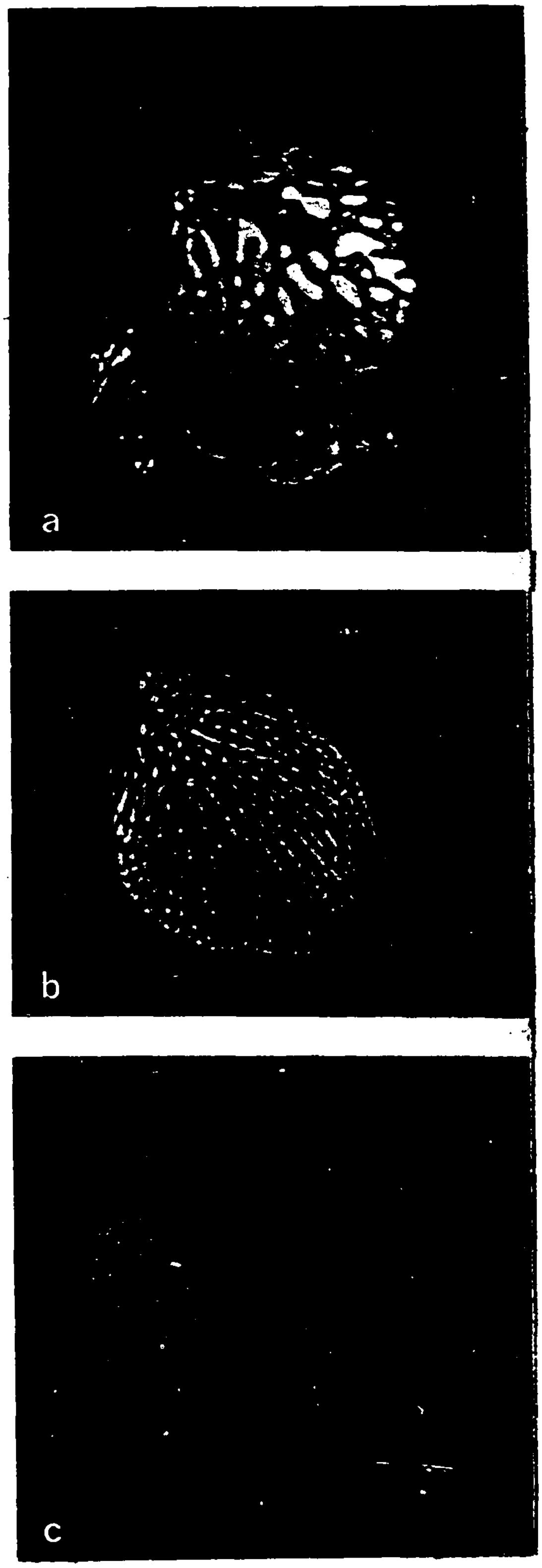

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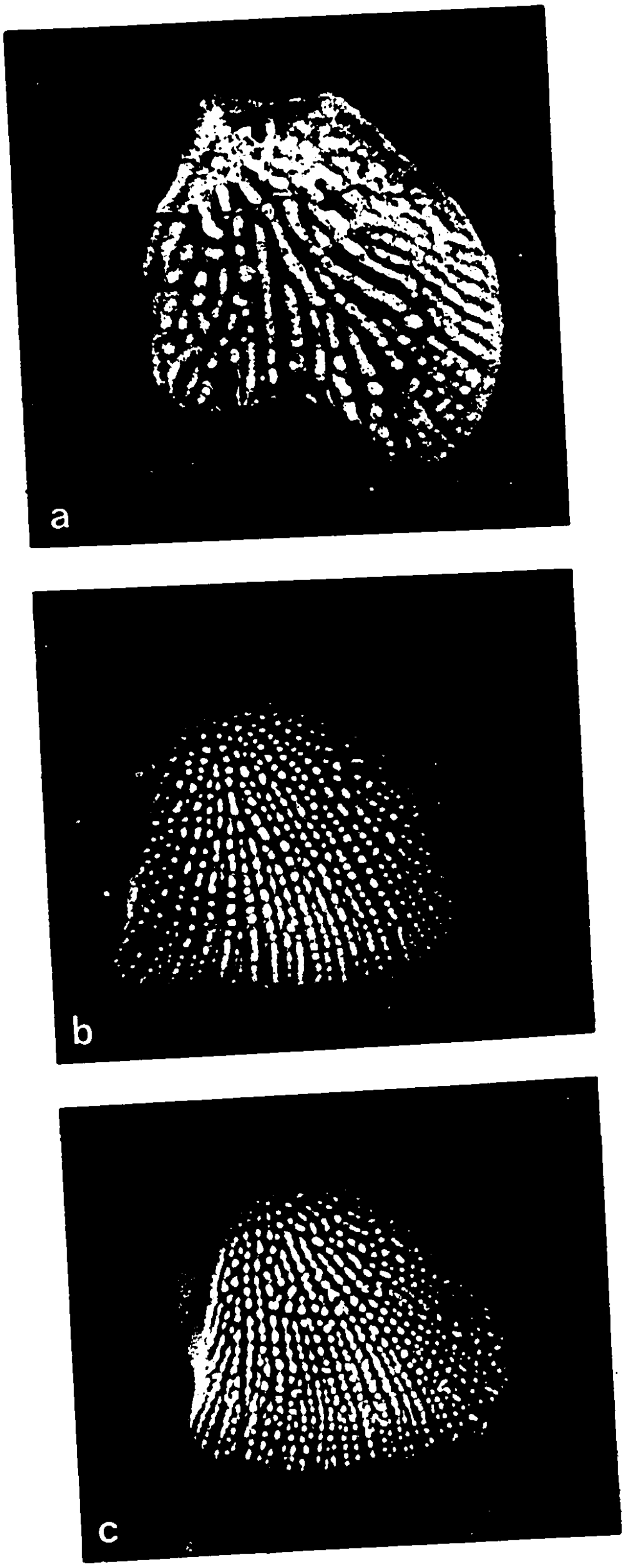

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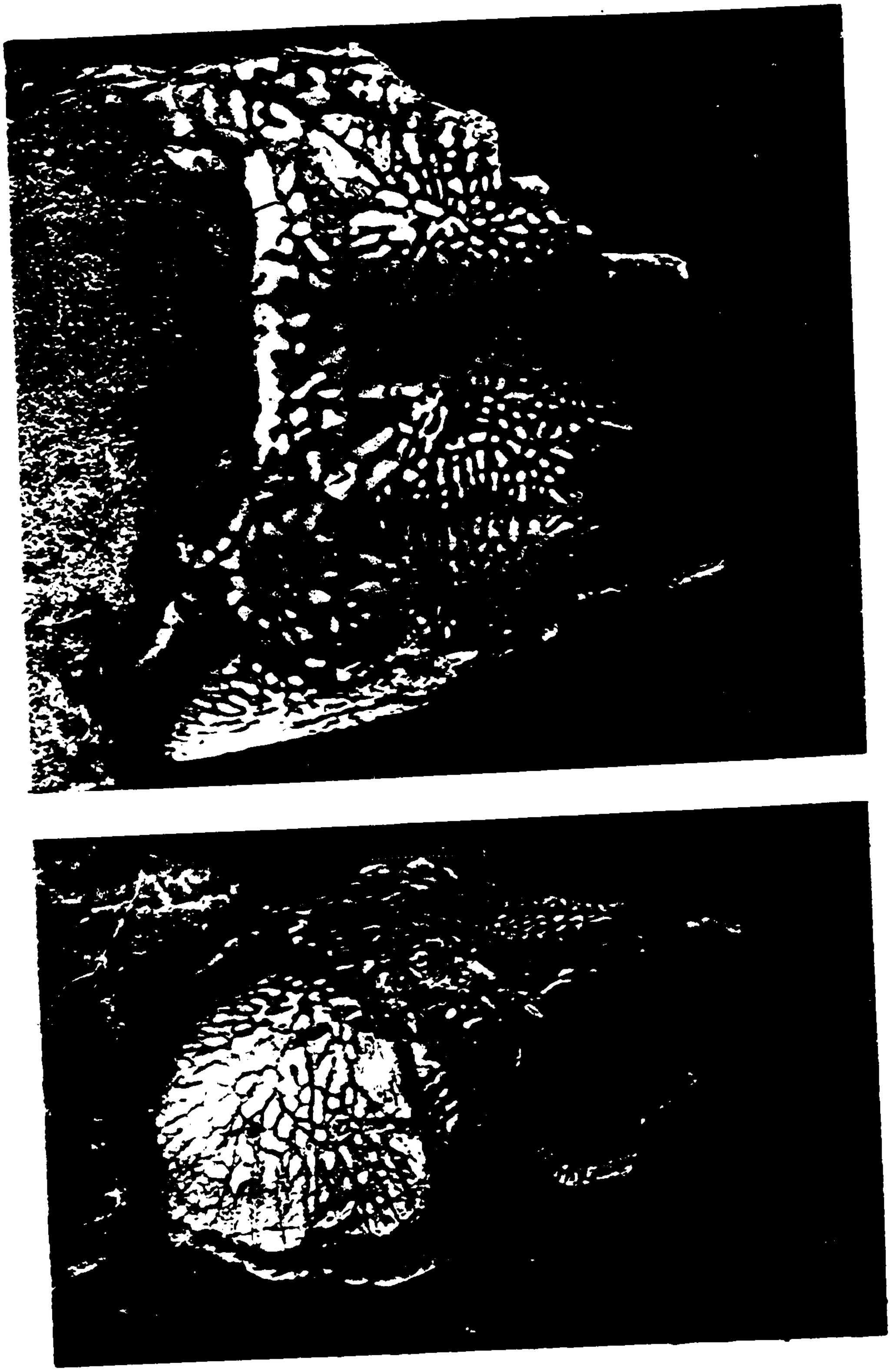

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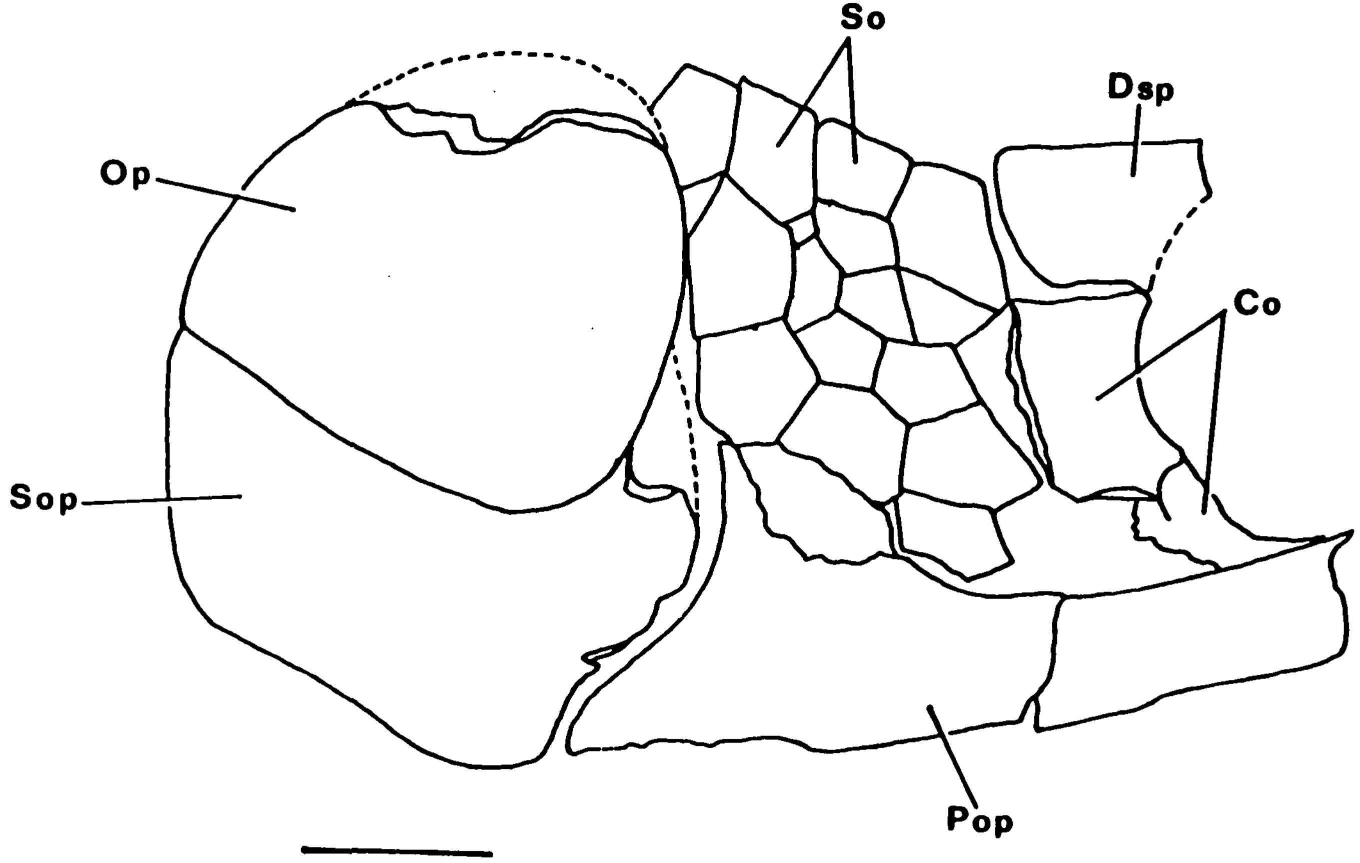

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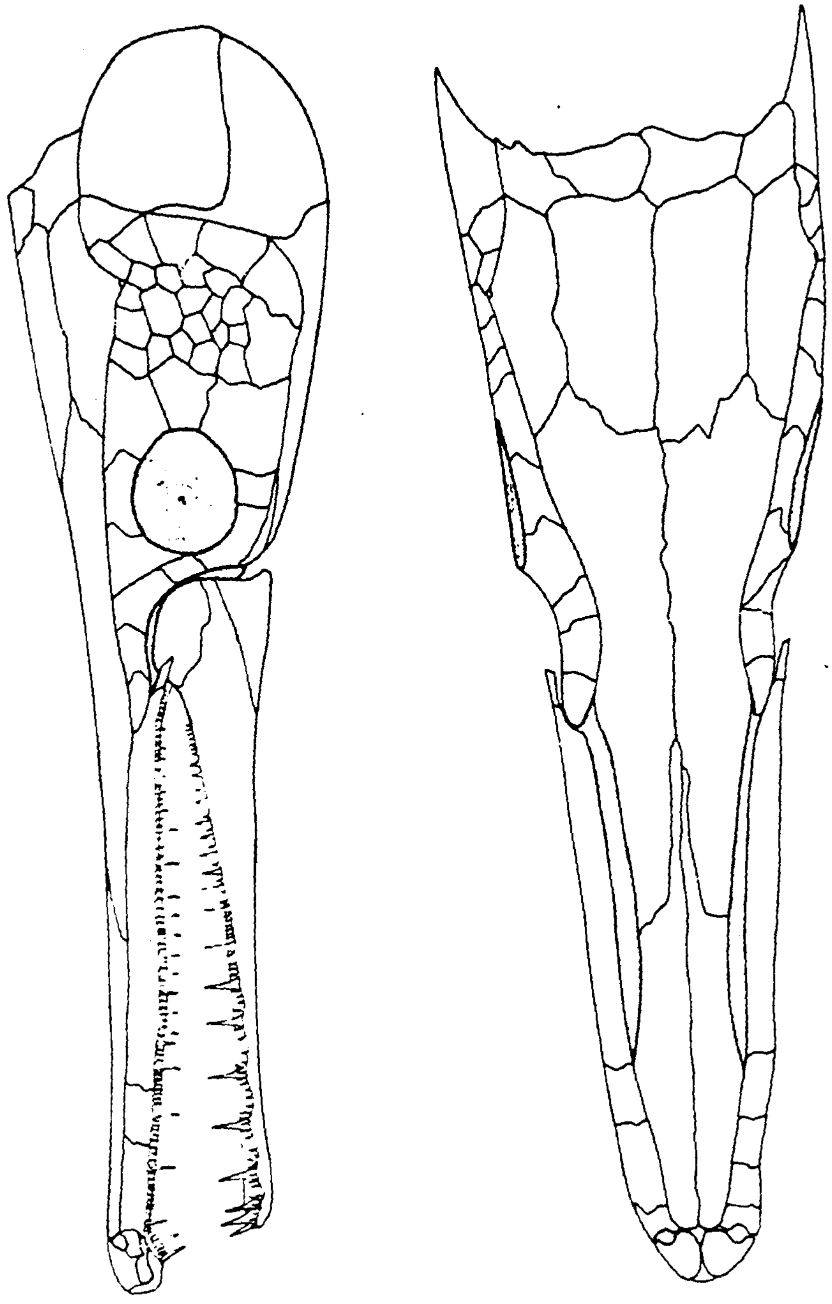


FIGURE 33

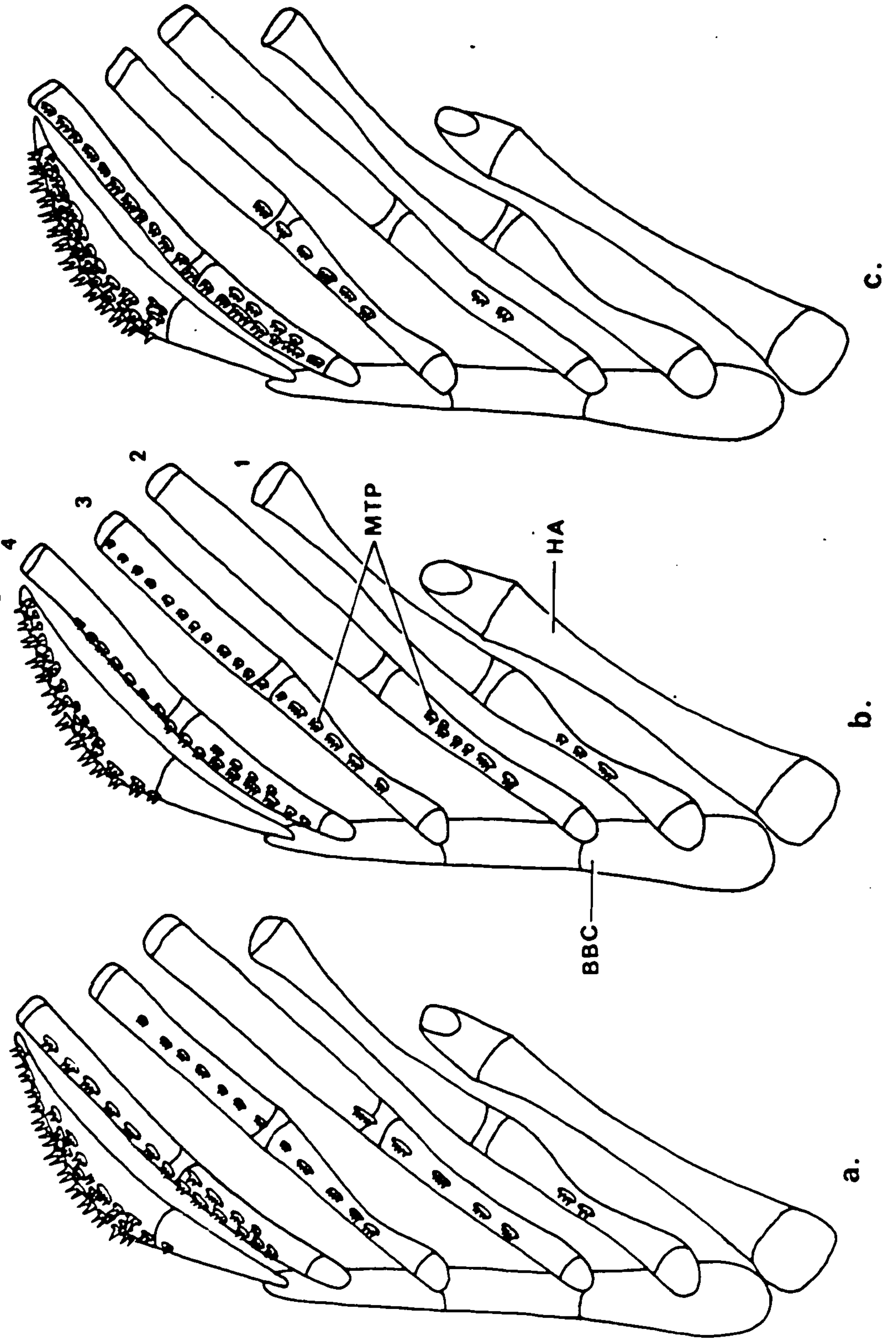


Fig. 34

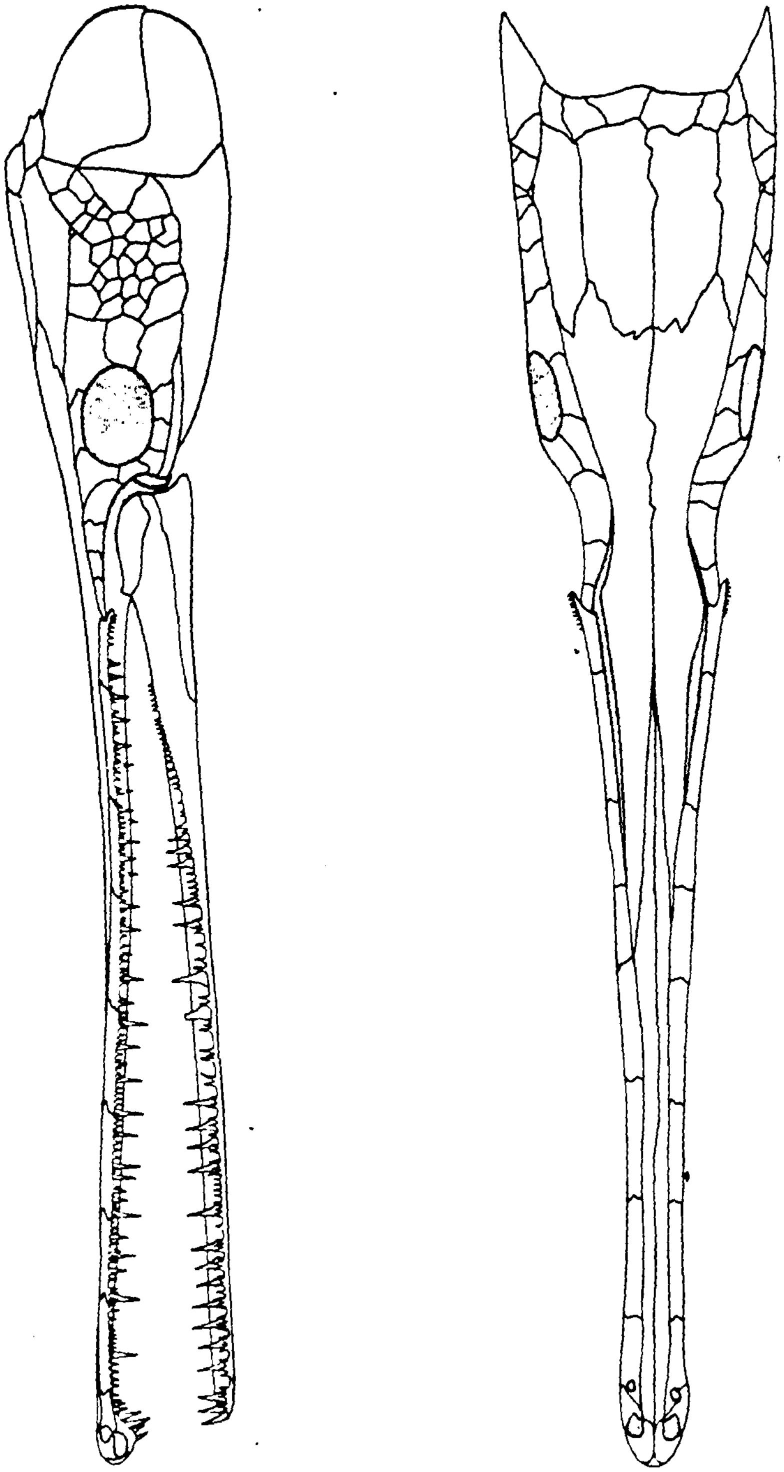
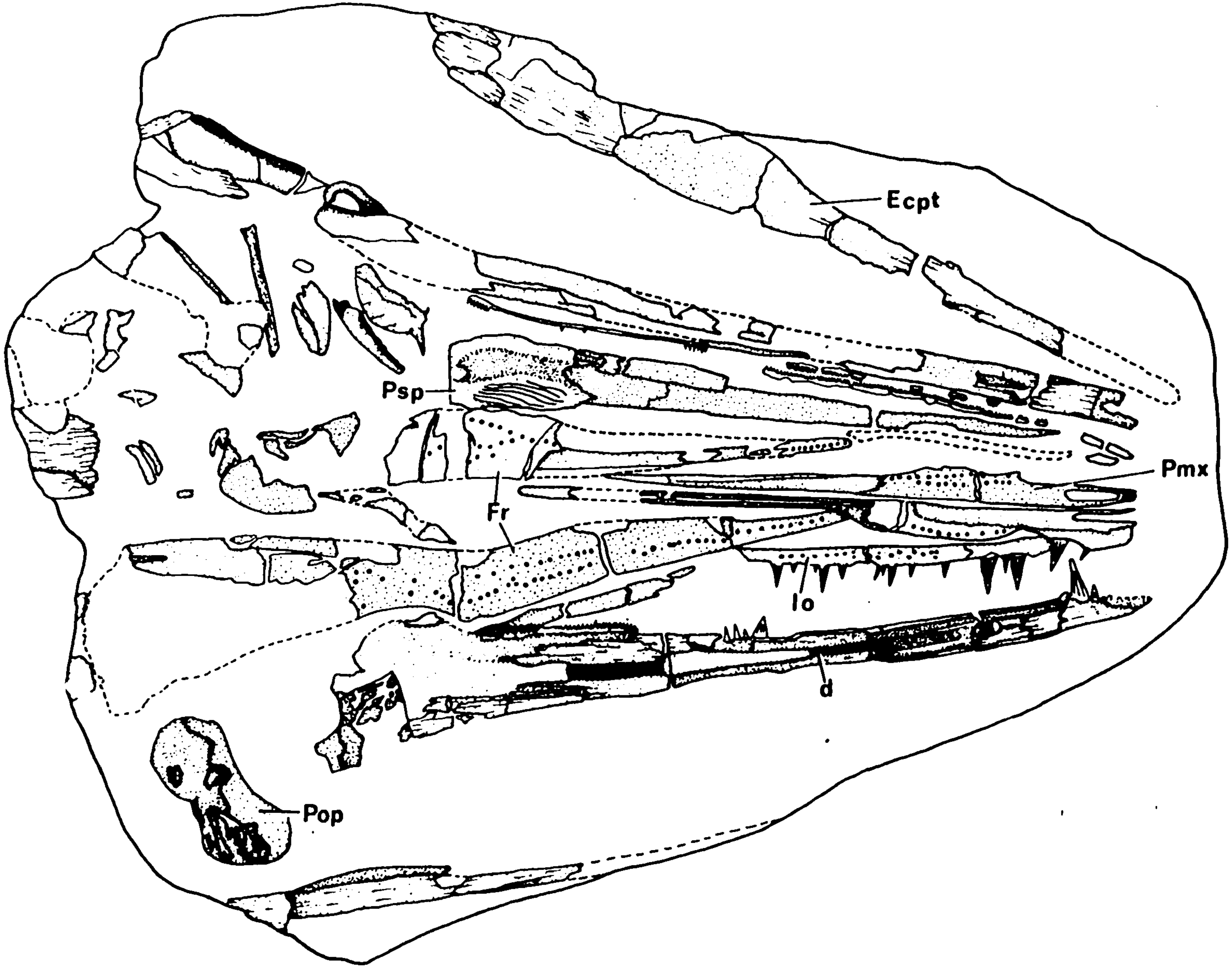


FIGURE 35



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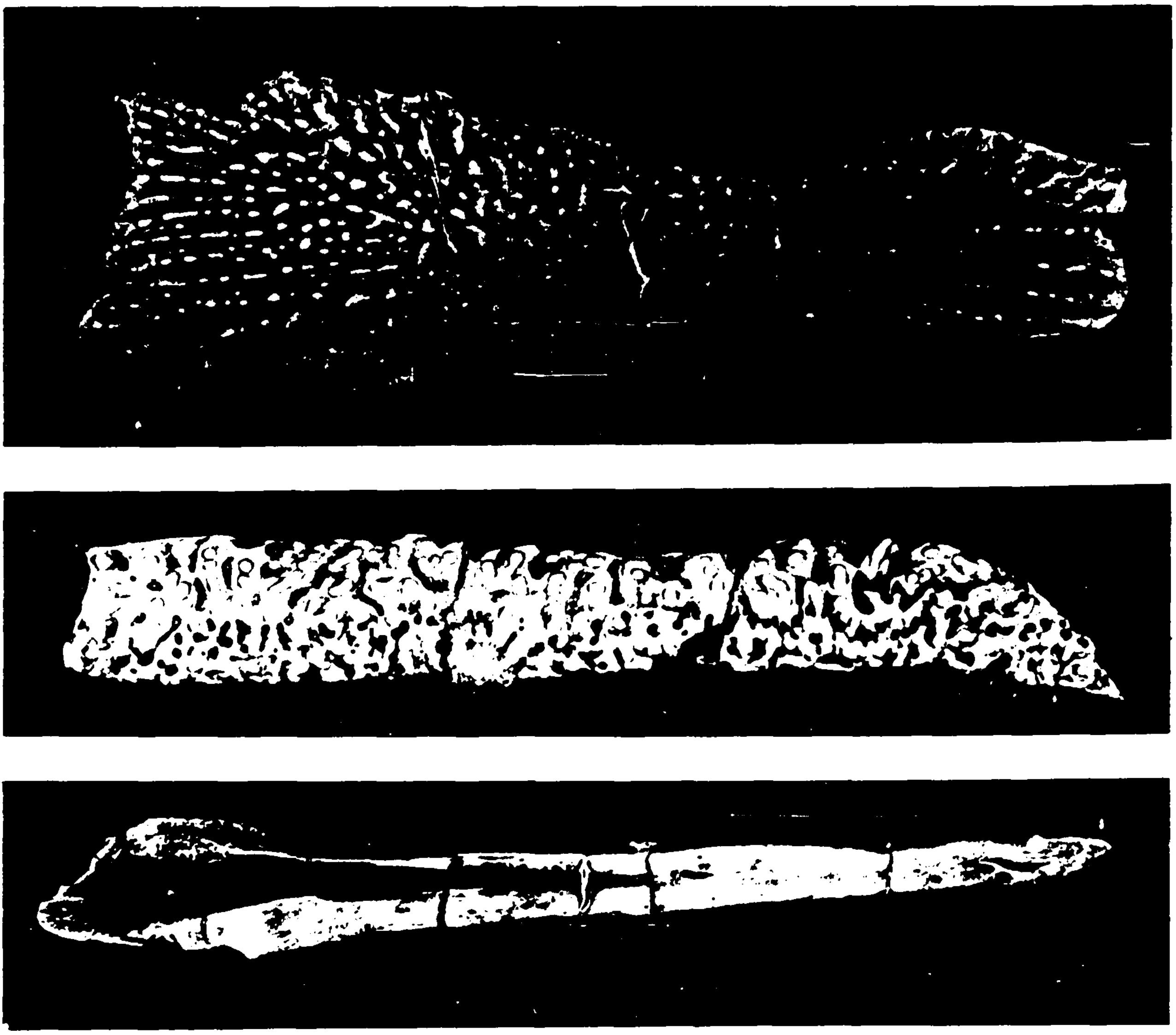

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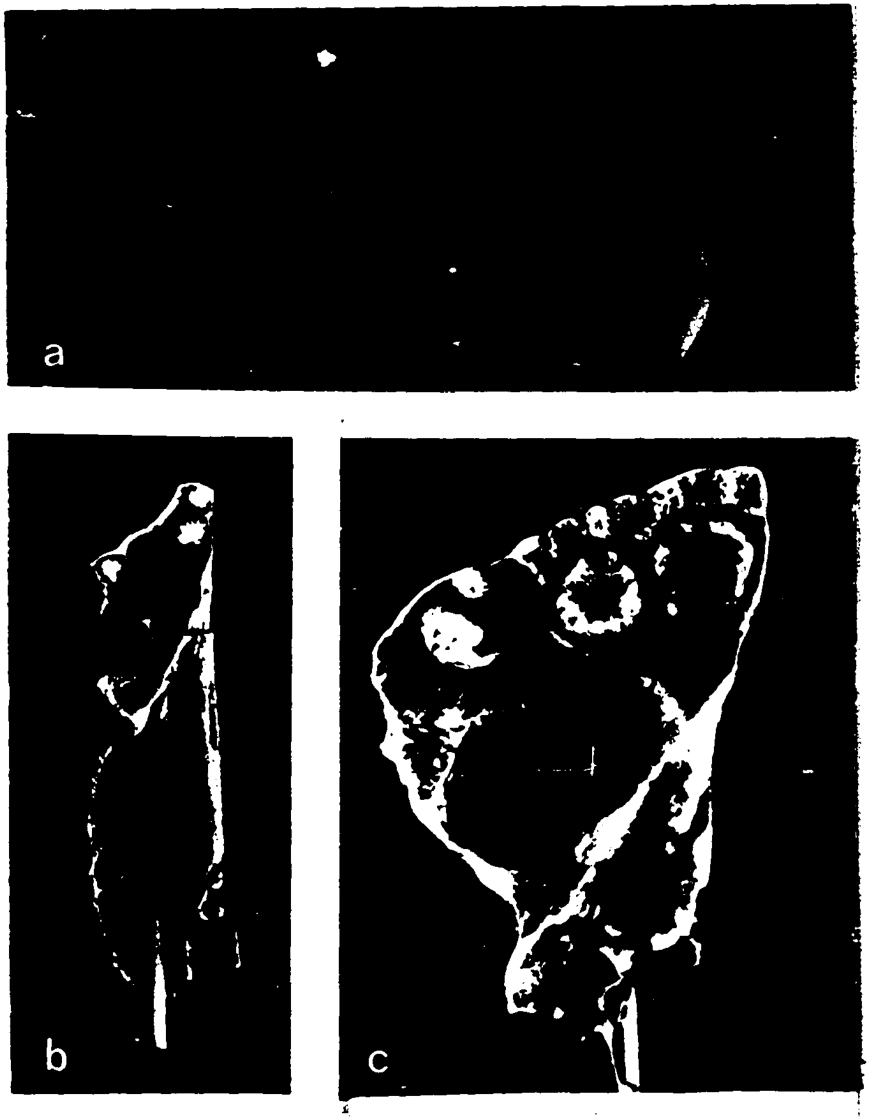

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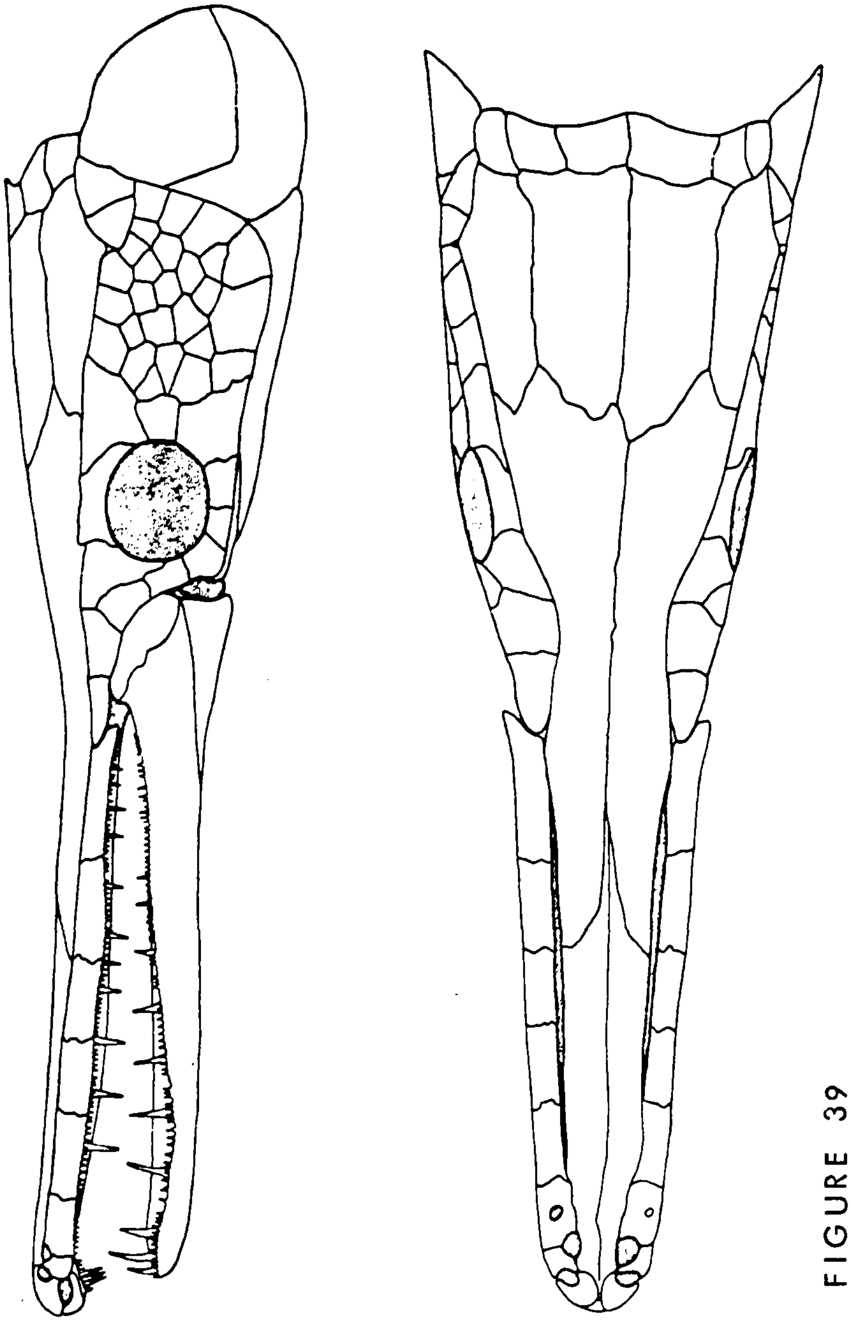

FIGURE 39

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FIGURE 41

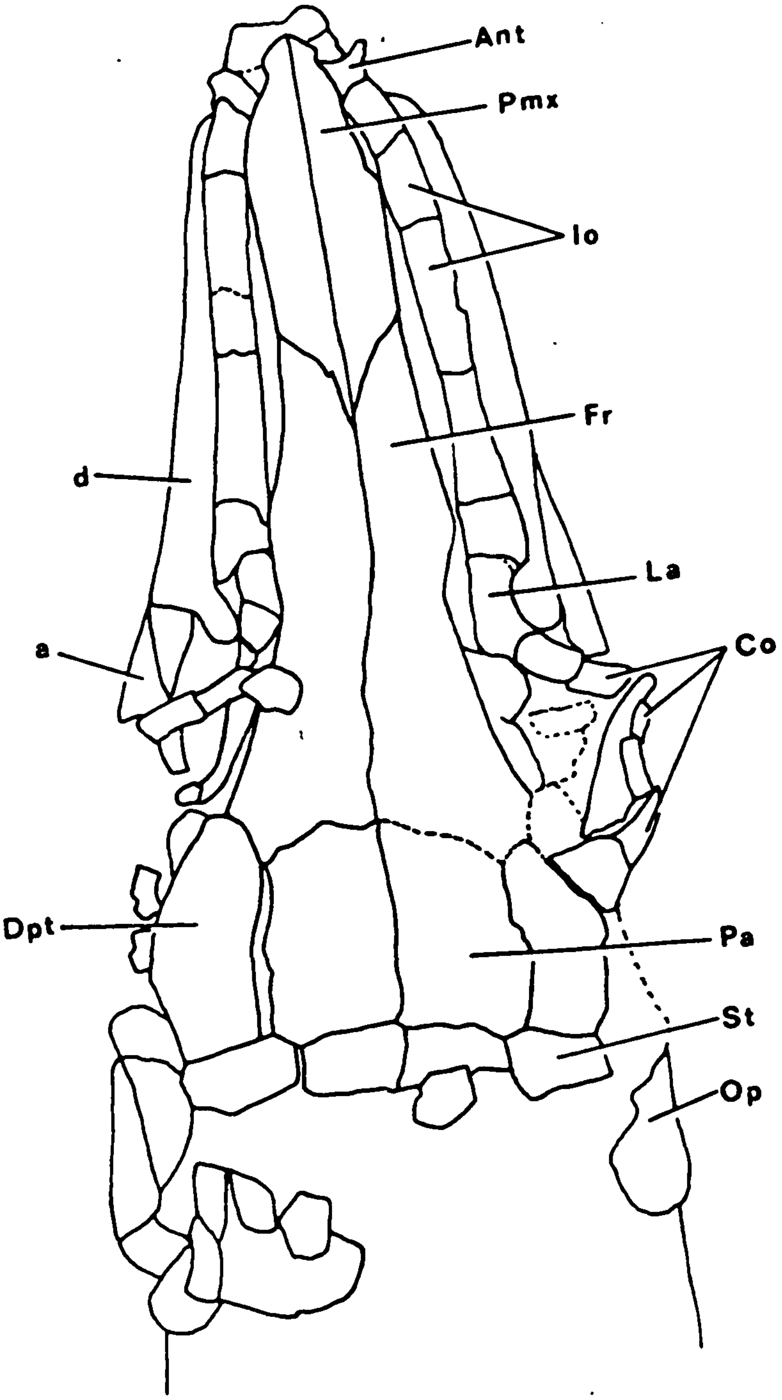


FIGURE 42

FIGURE 43

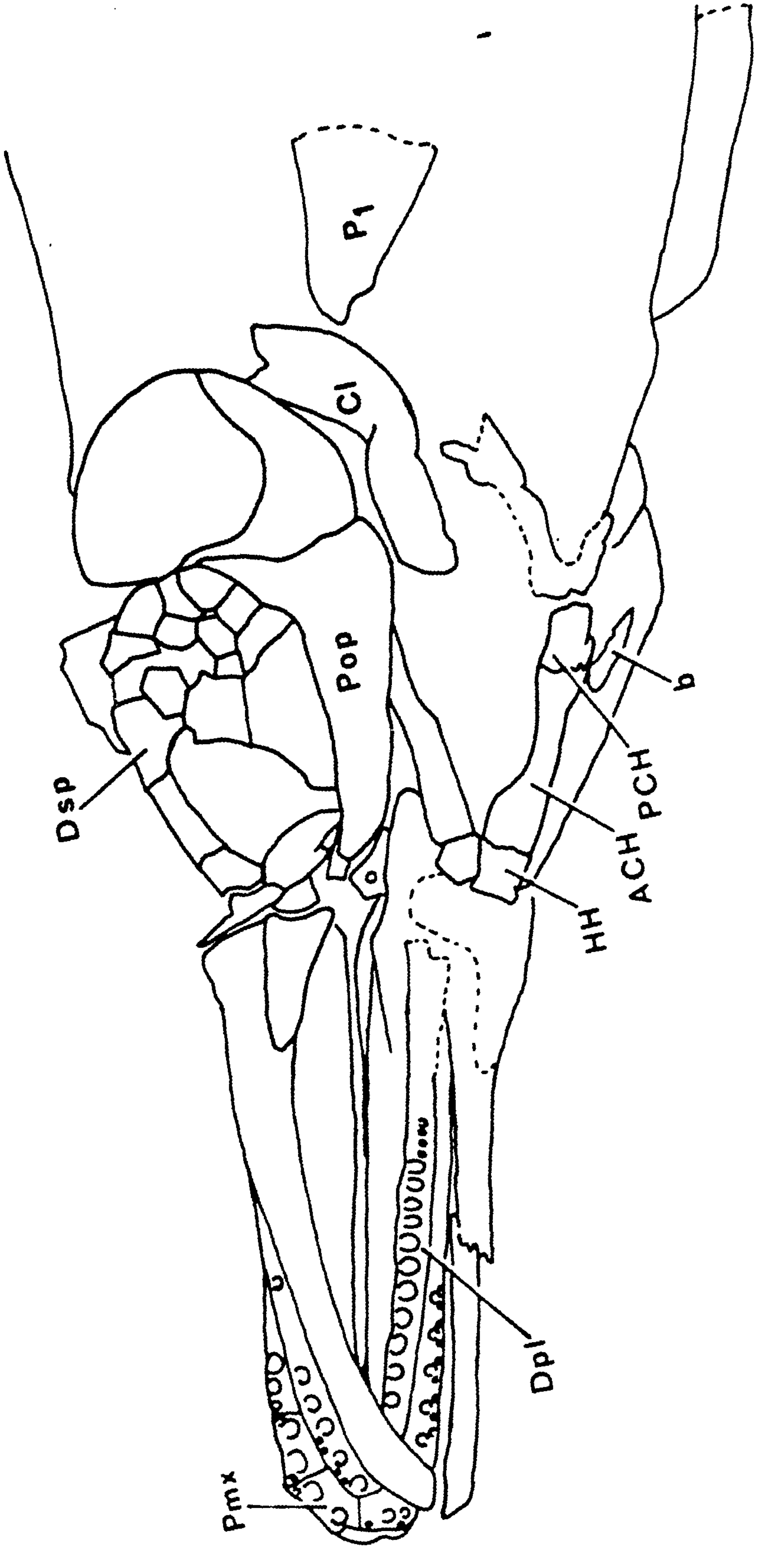
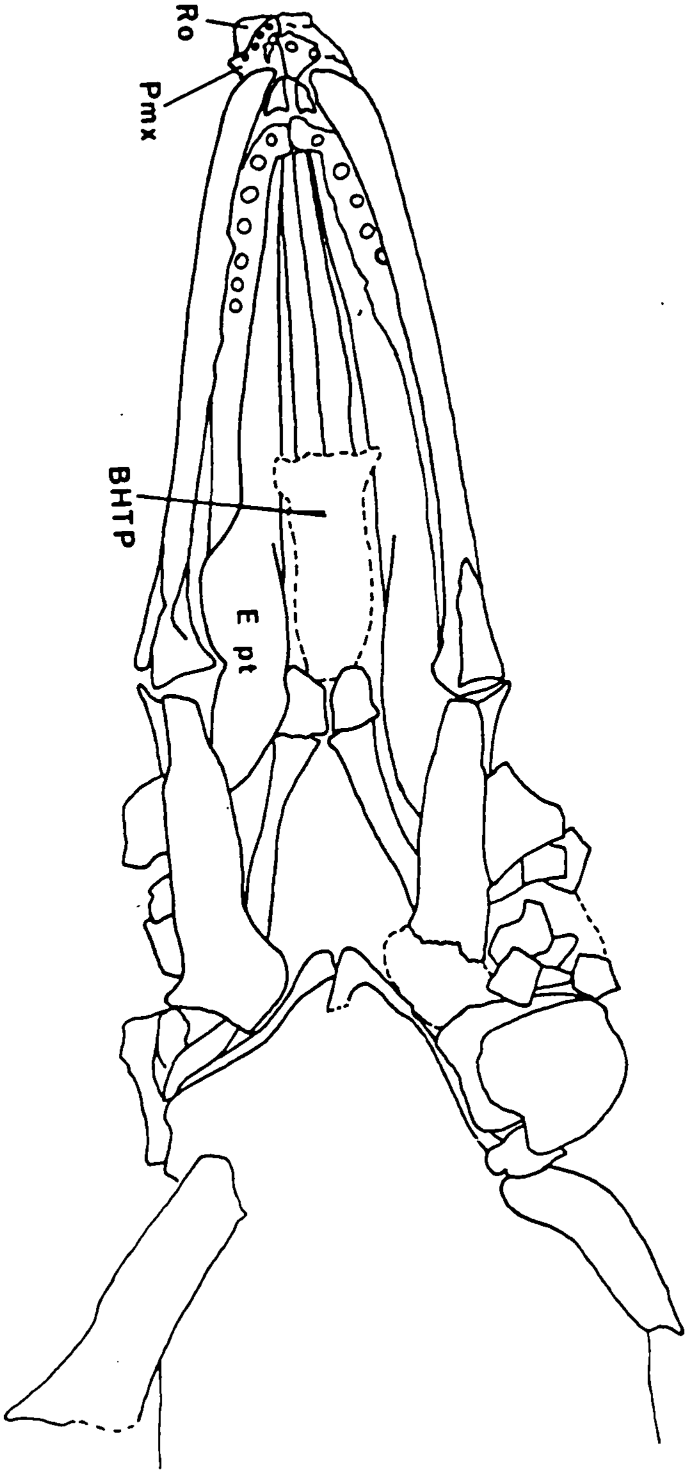


FIGURE 44

FIGURE 45



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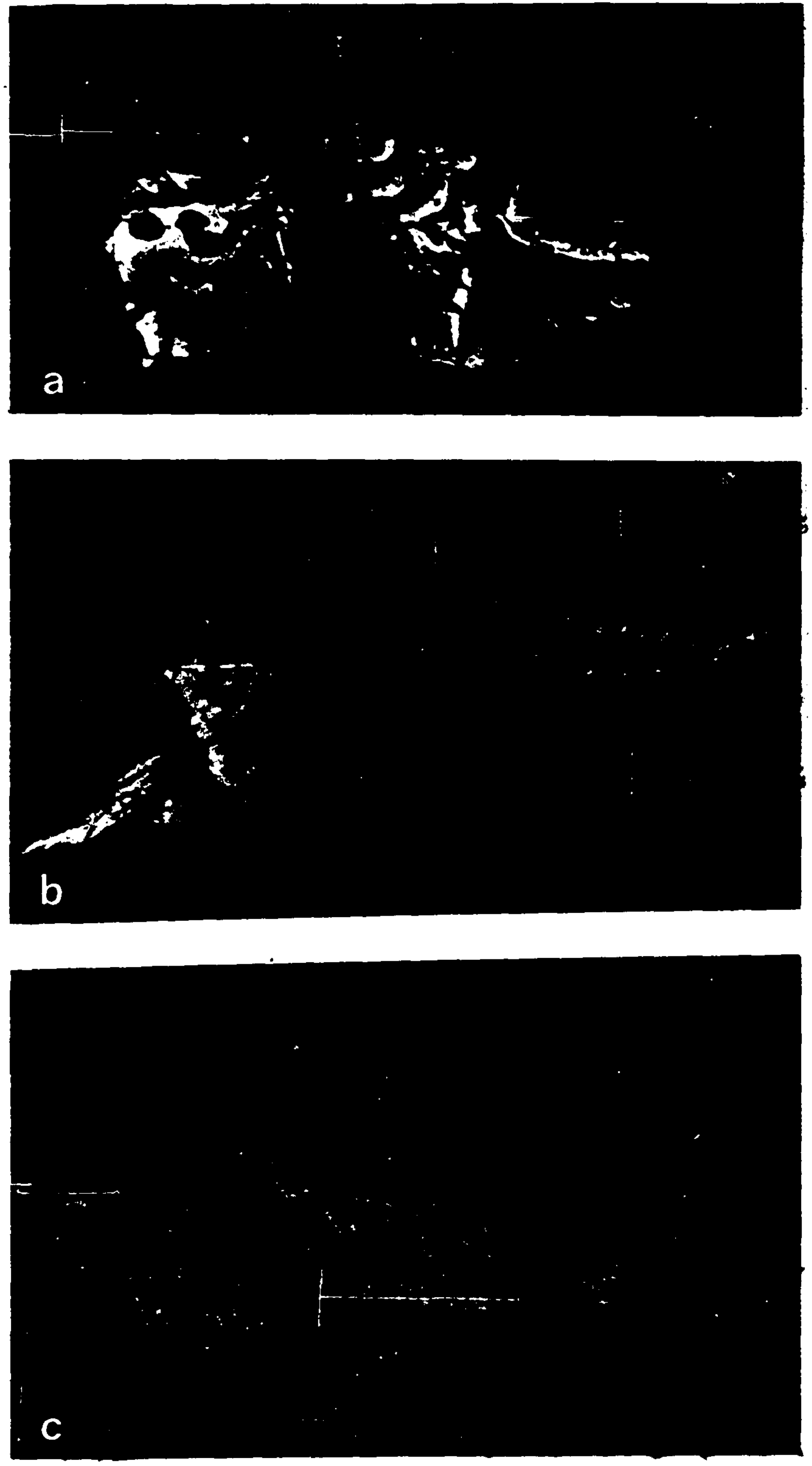

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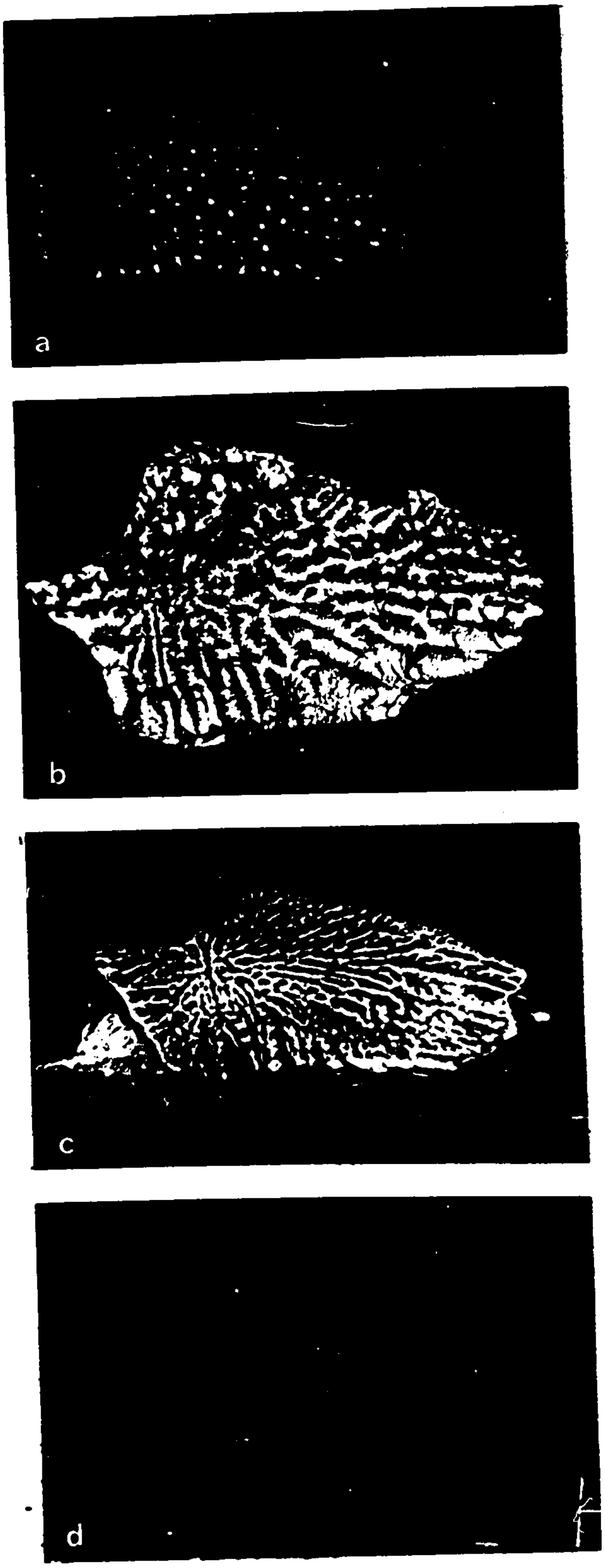

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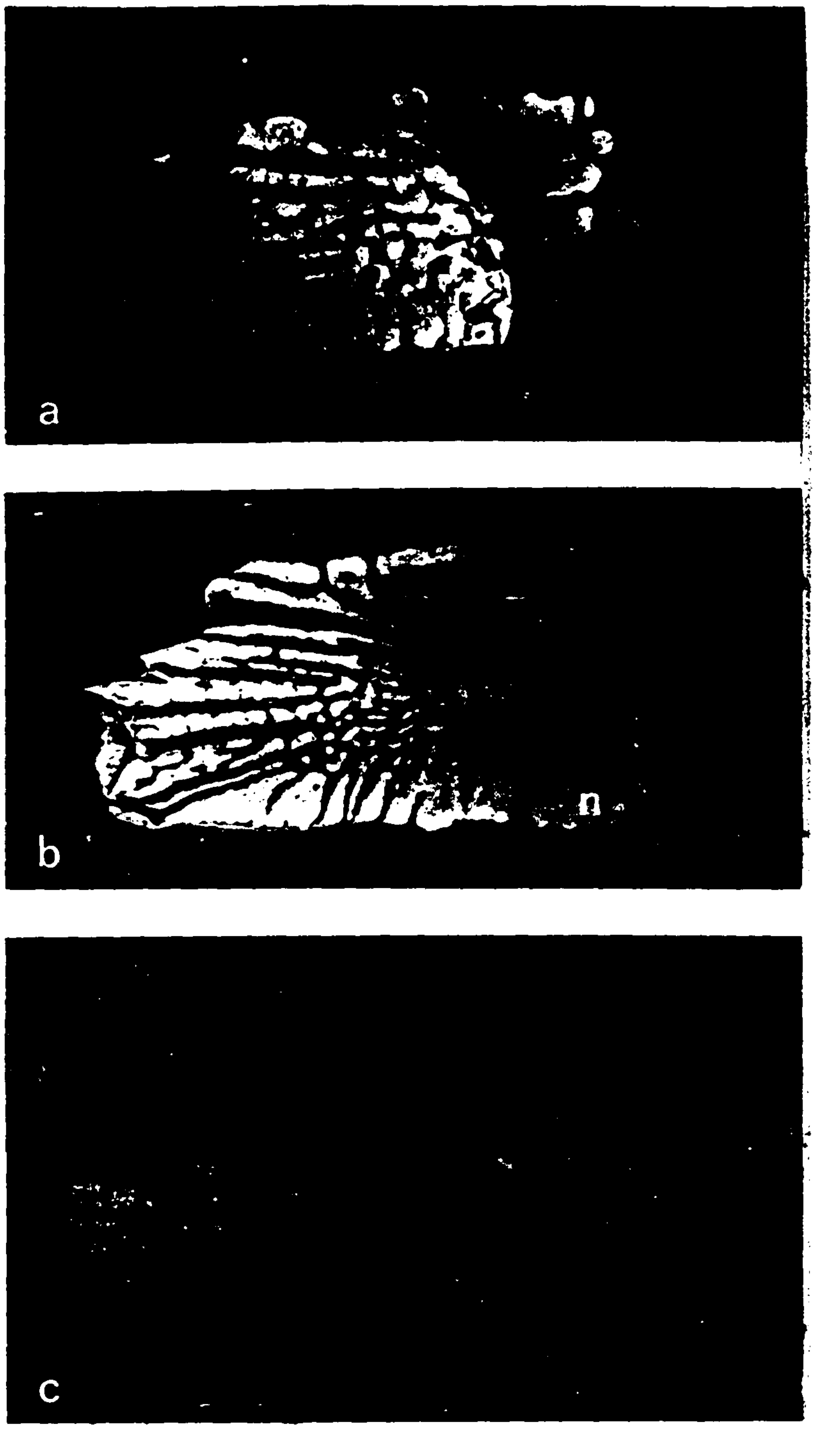

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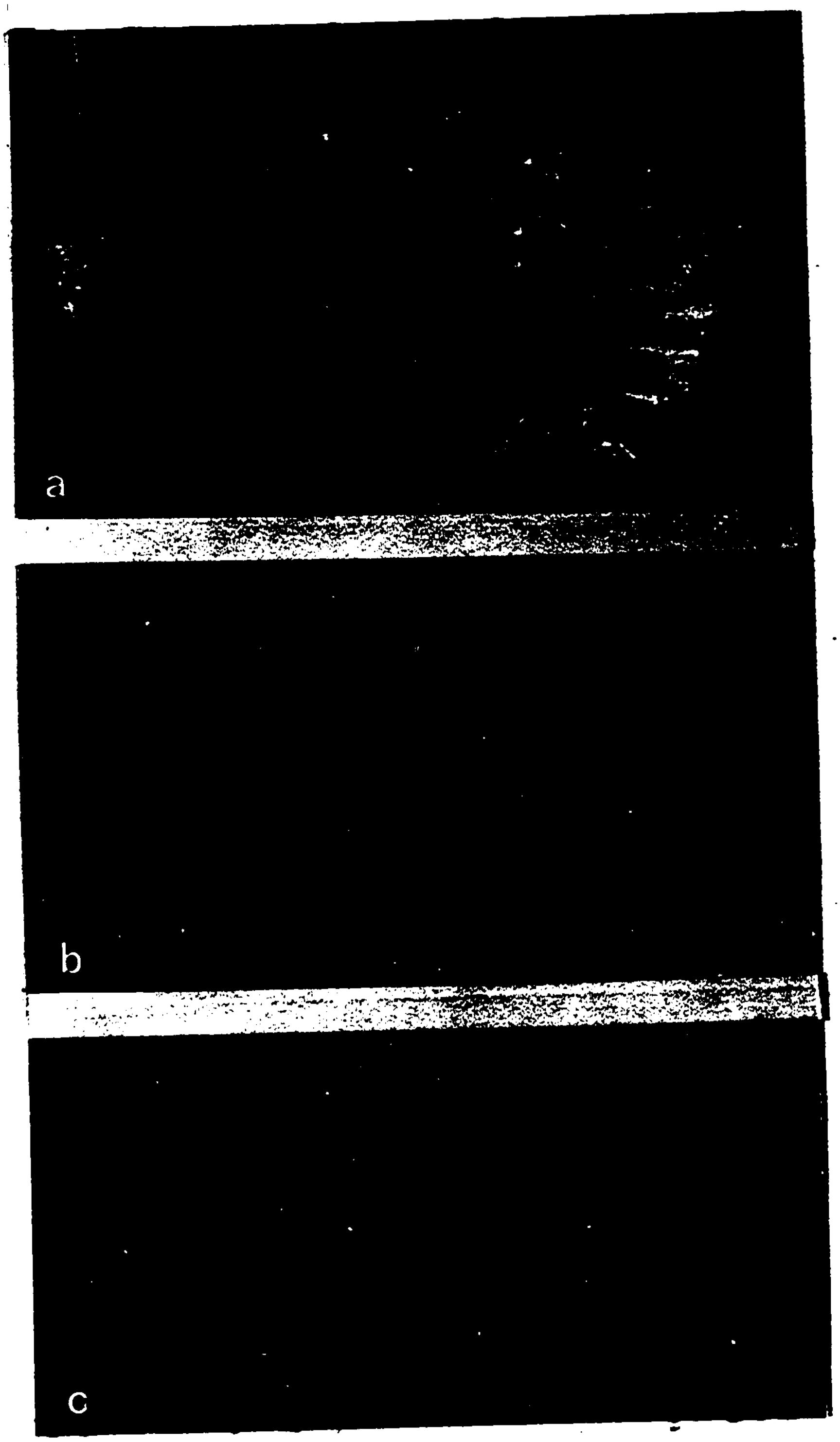
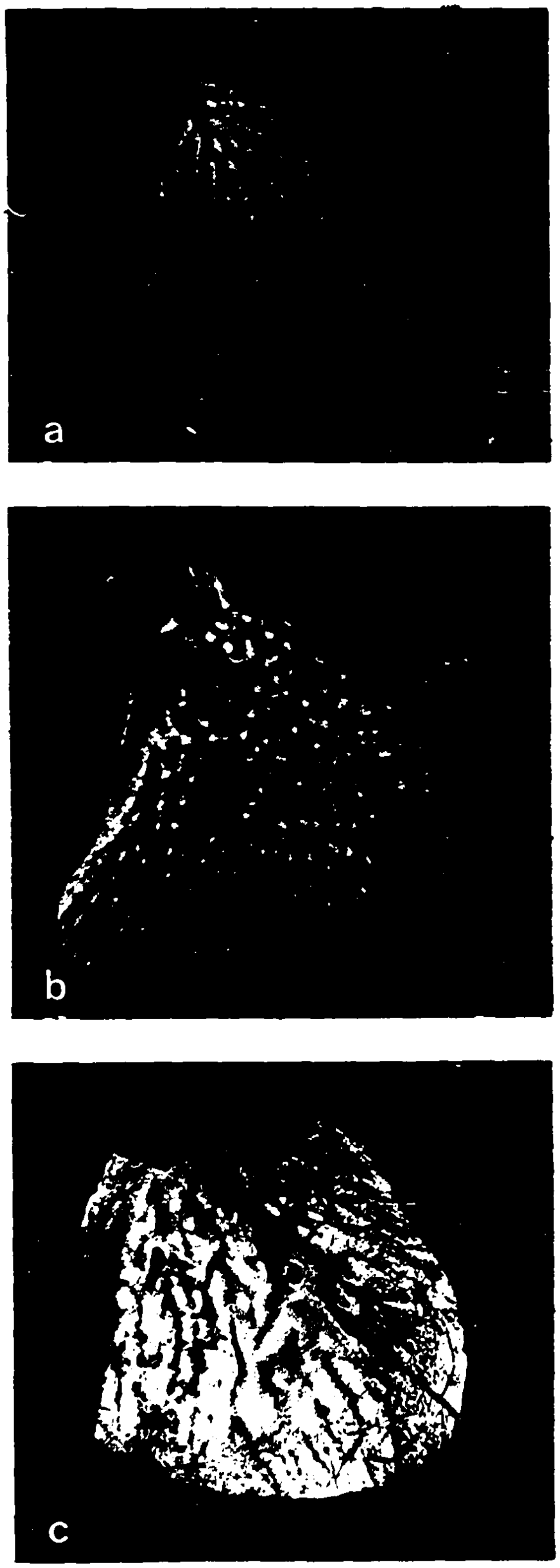


FIGURE 50



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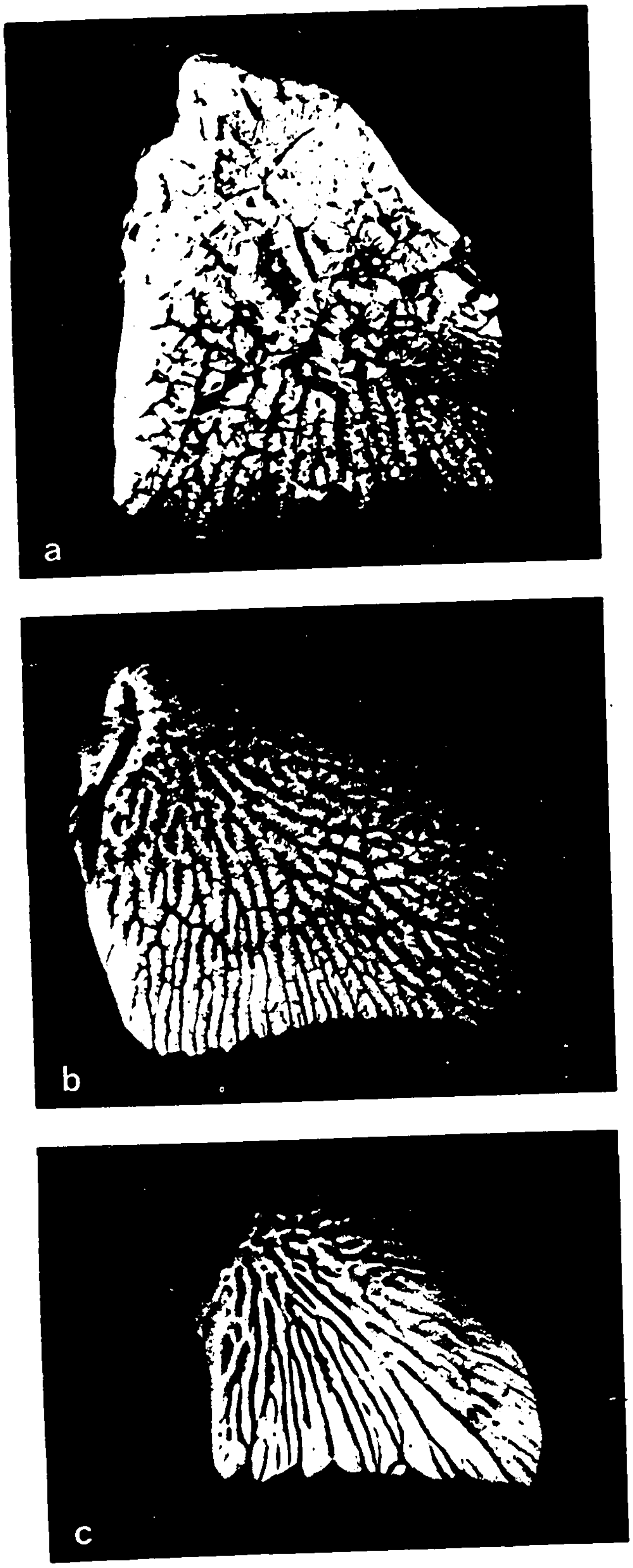

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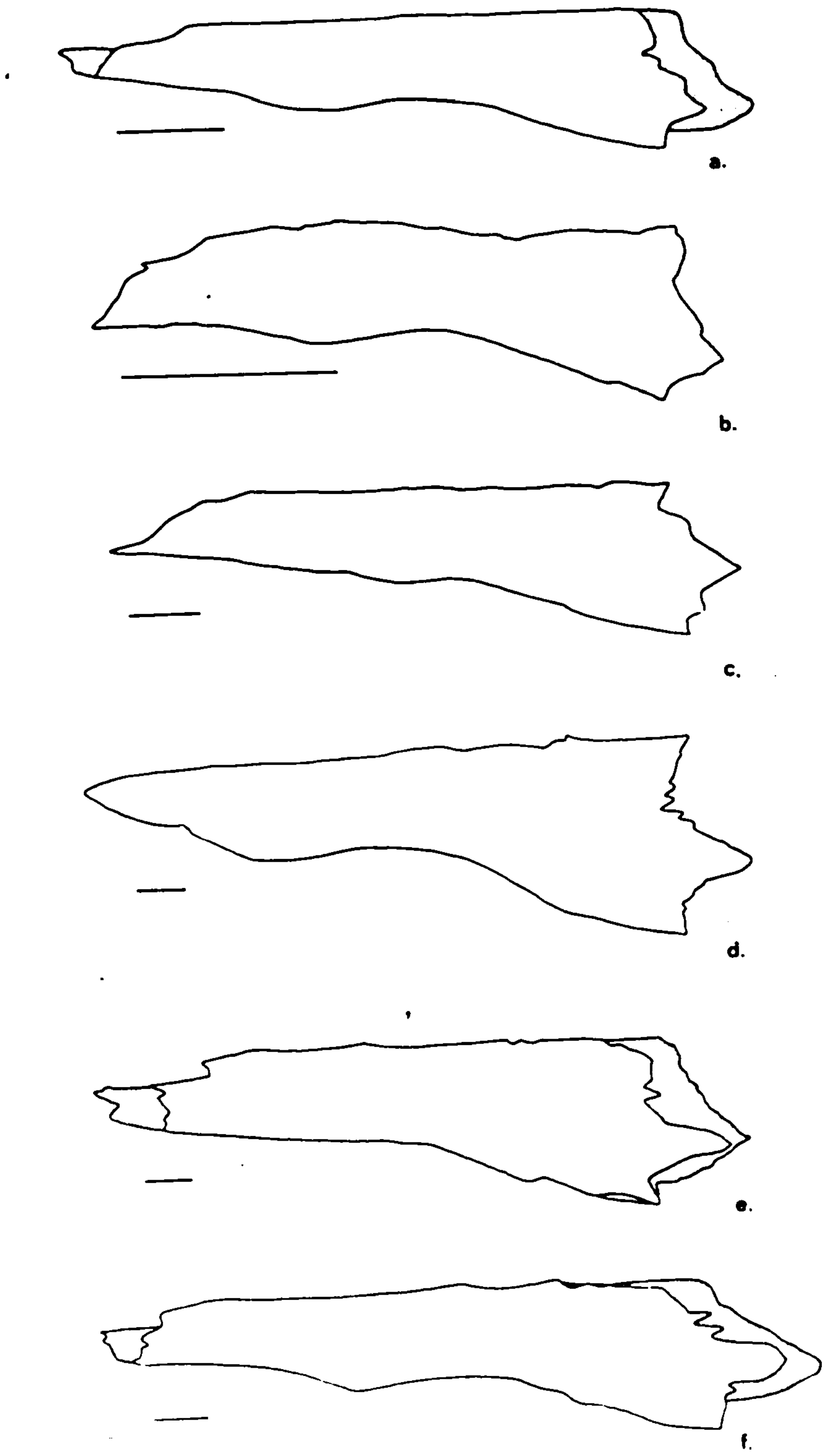

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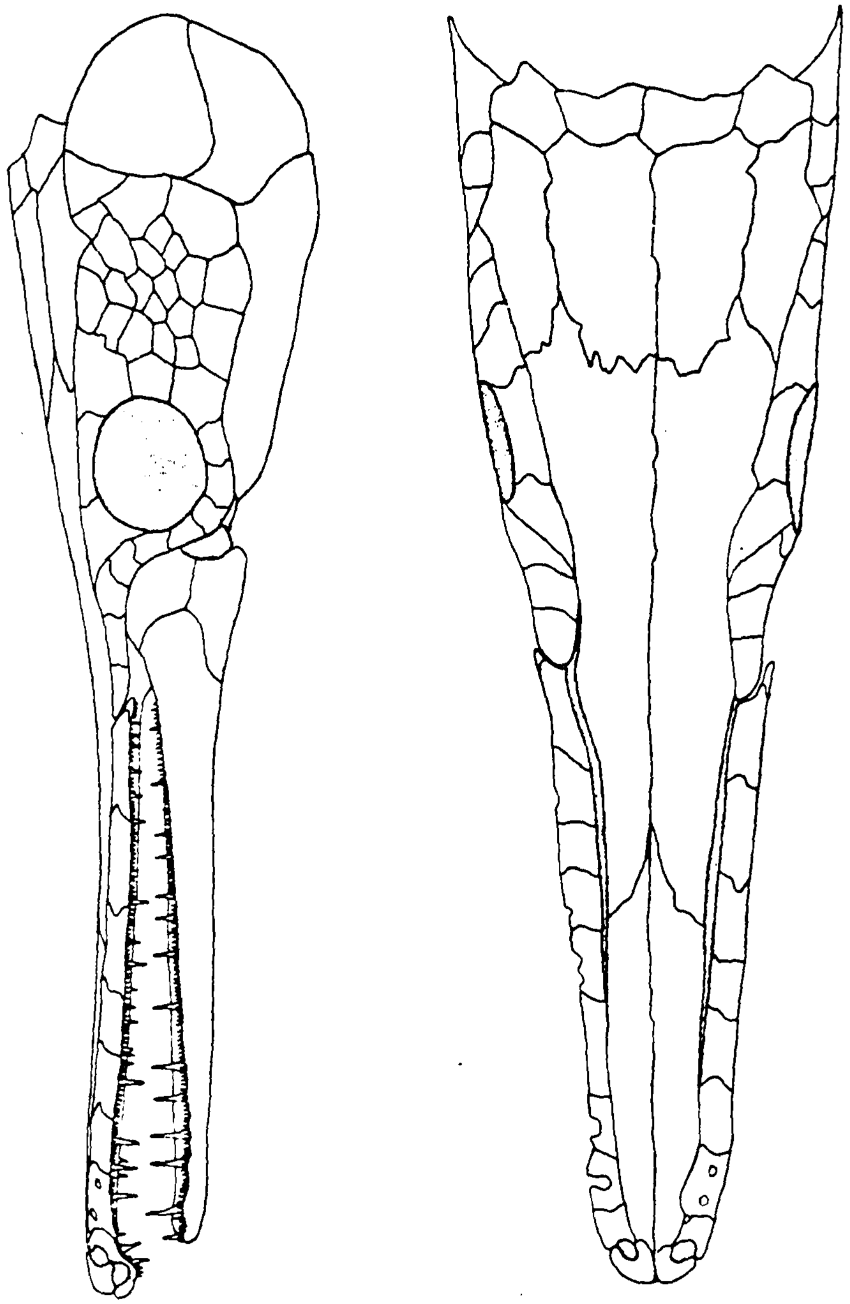

FIGURE 54

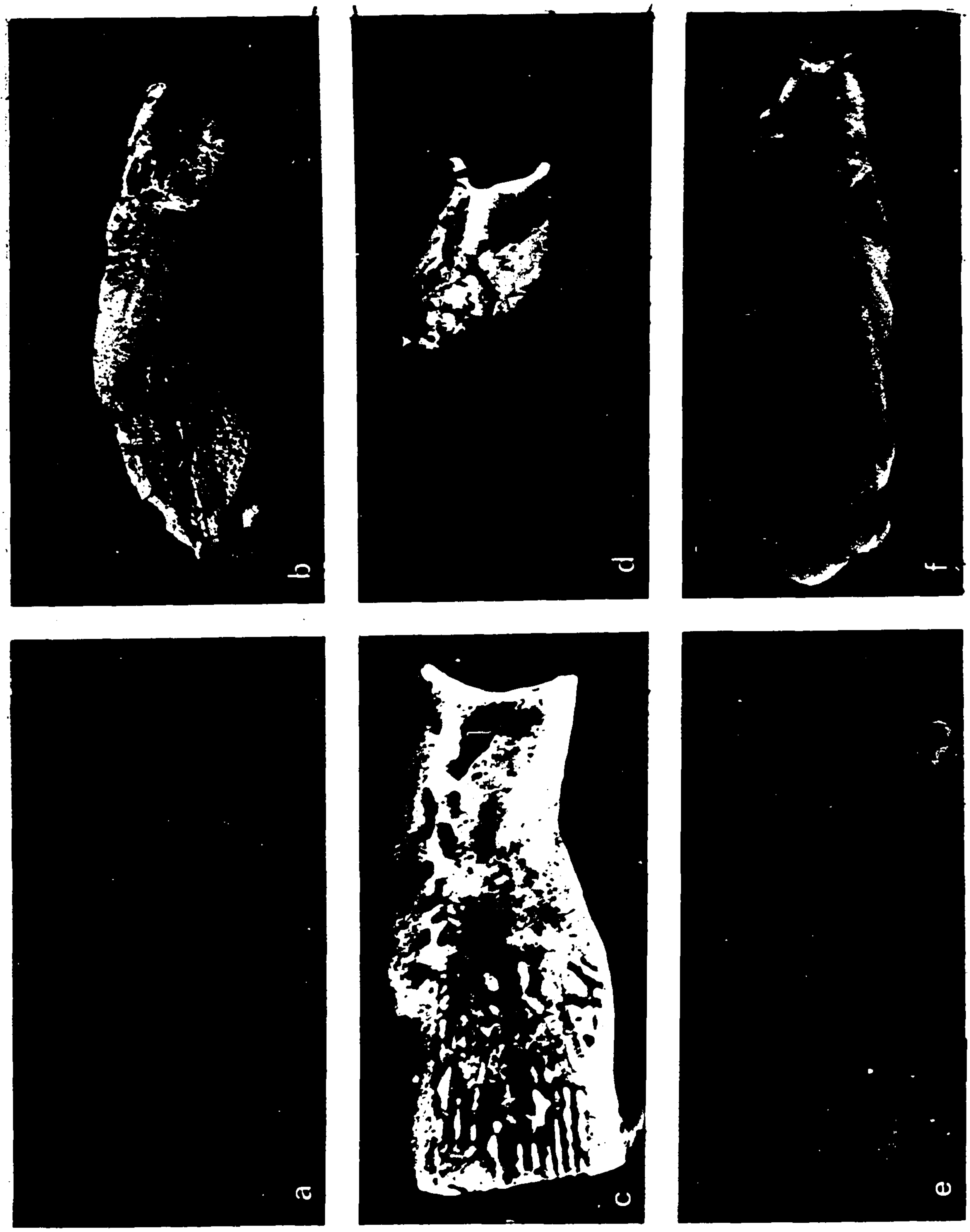

FIGURE 55

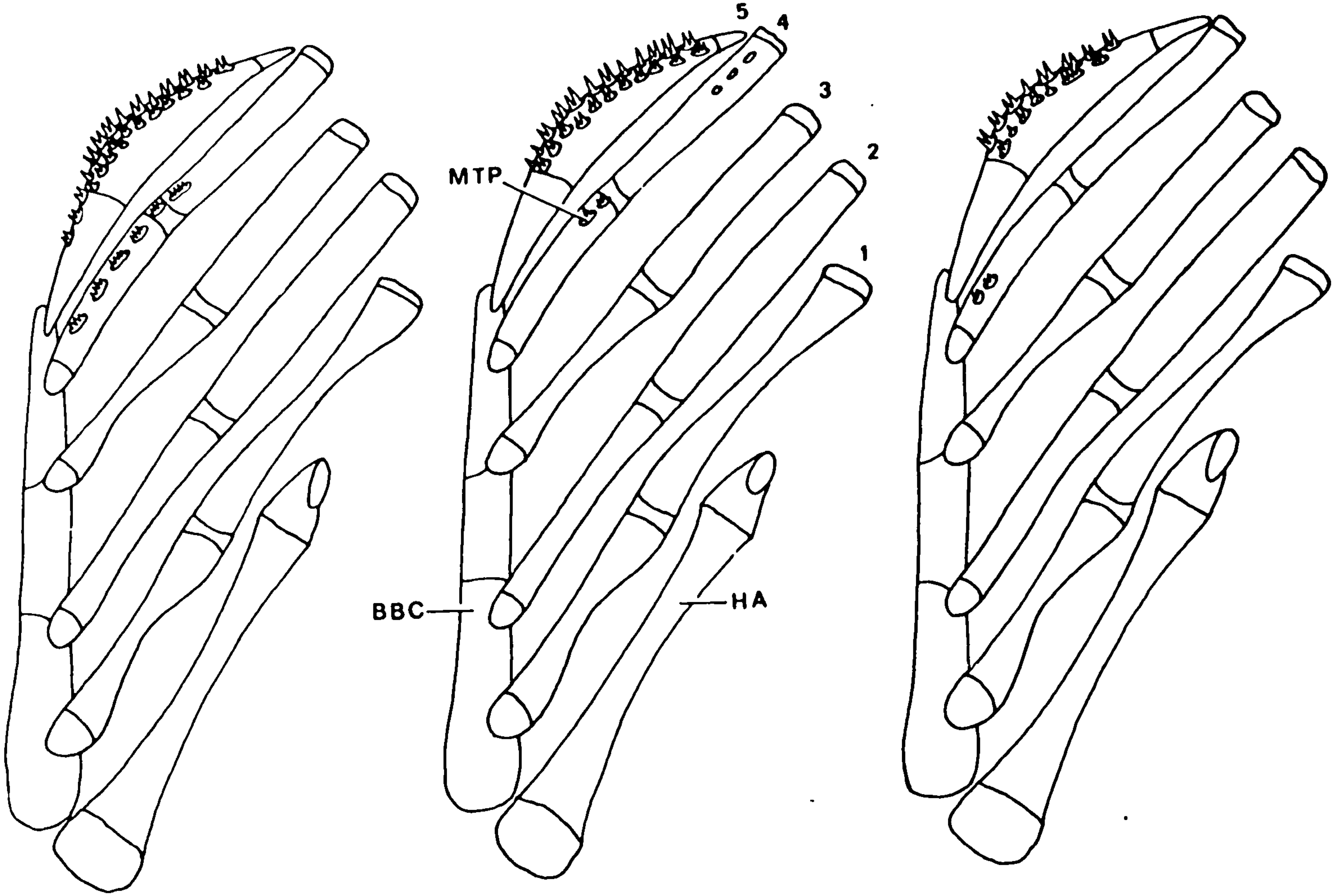

FIGURE 56

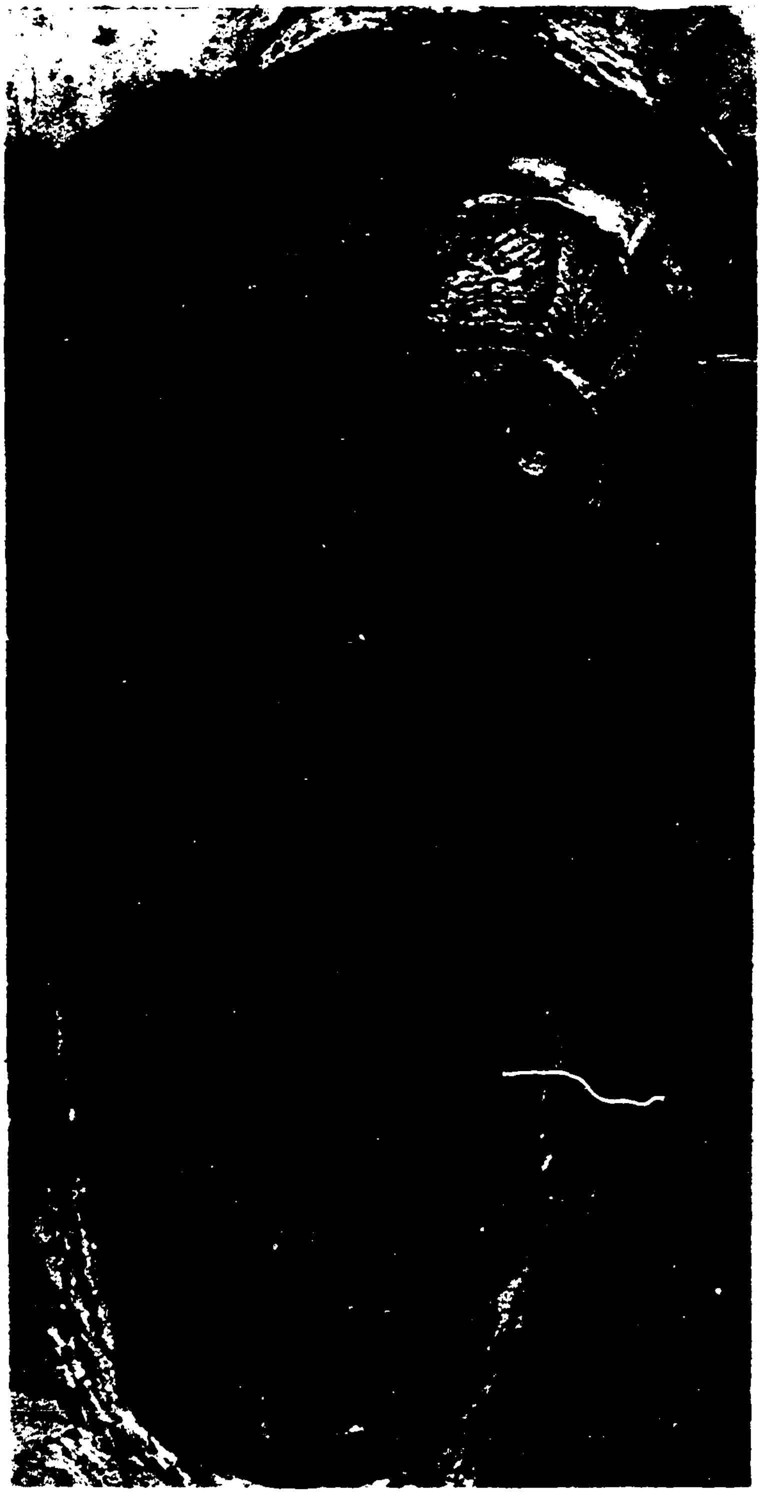

FIGURE 57

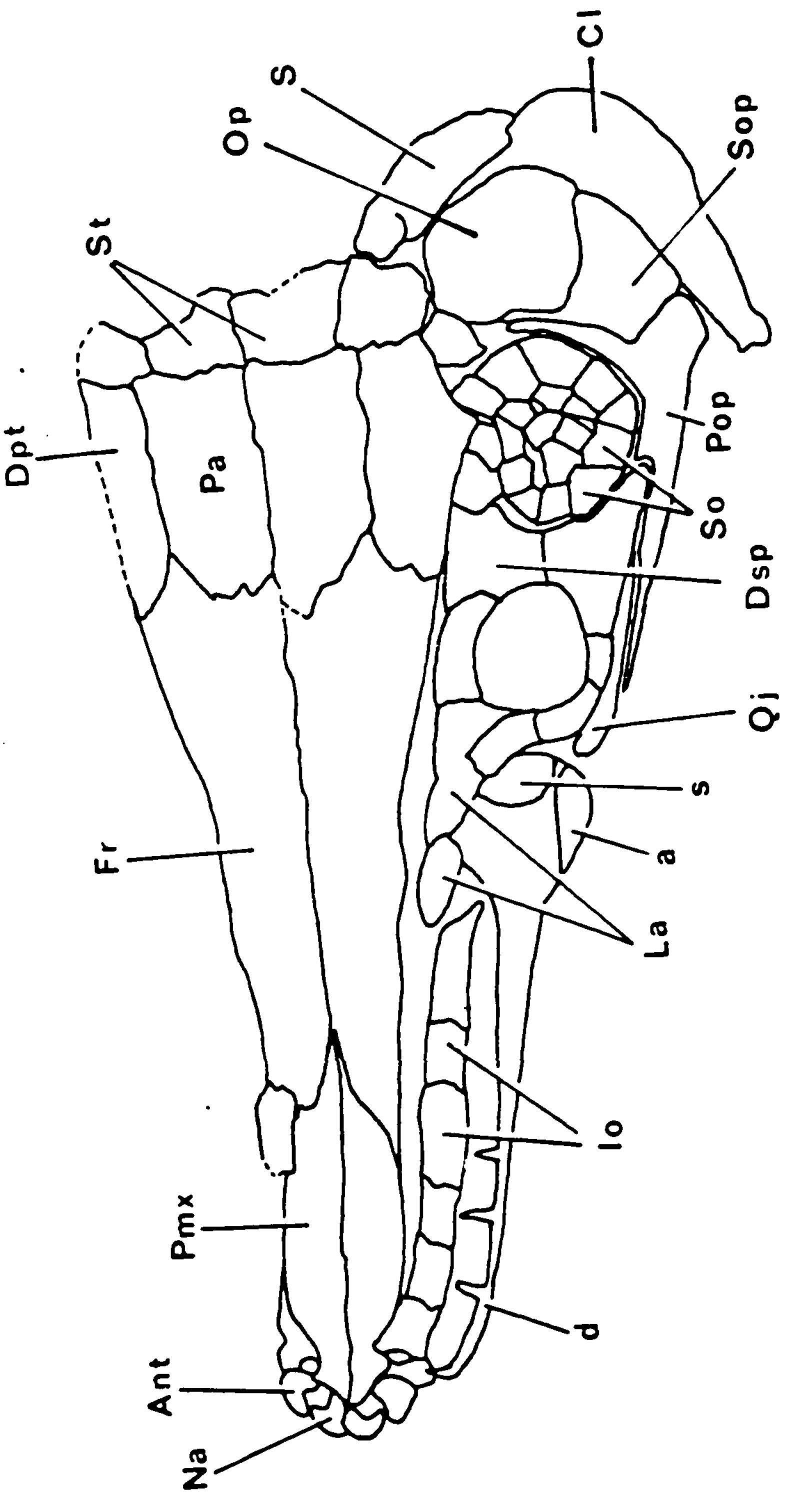

FIGURE 58

FIGURE 59

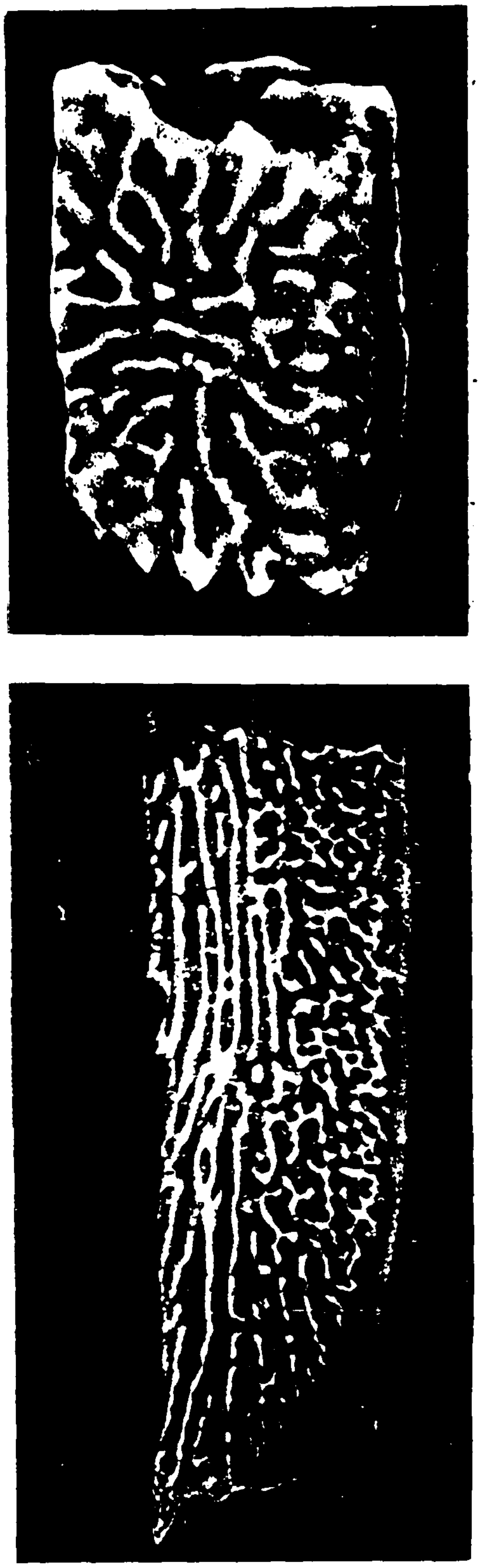

FIGURE 60

FIGURE 61

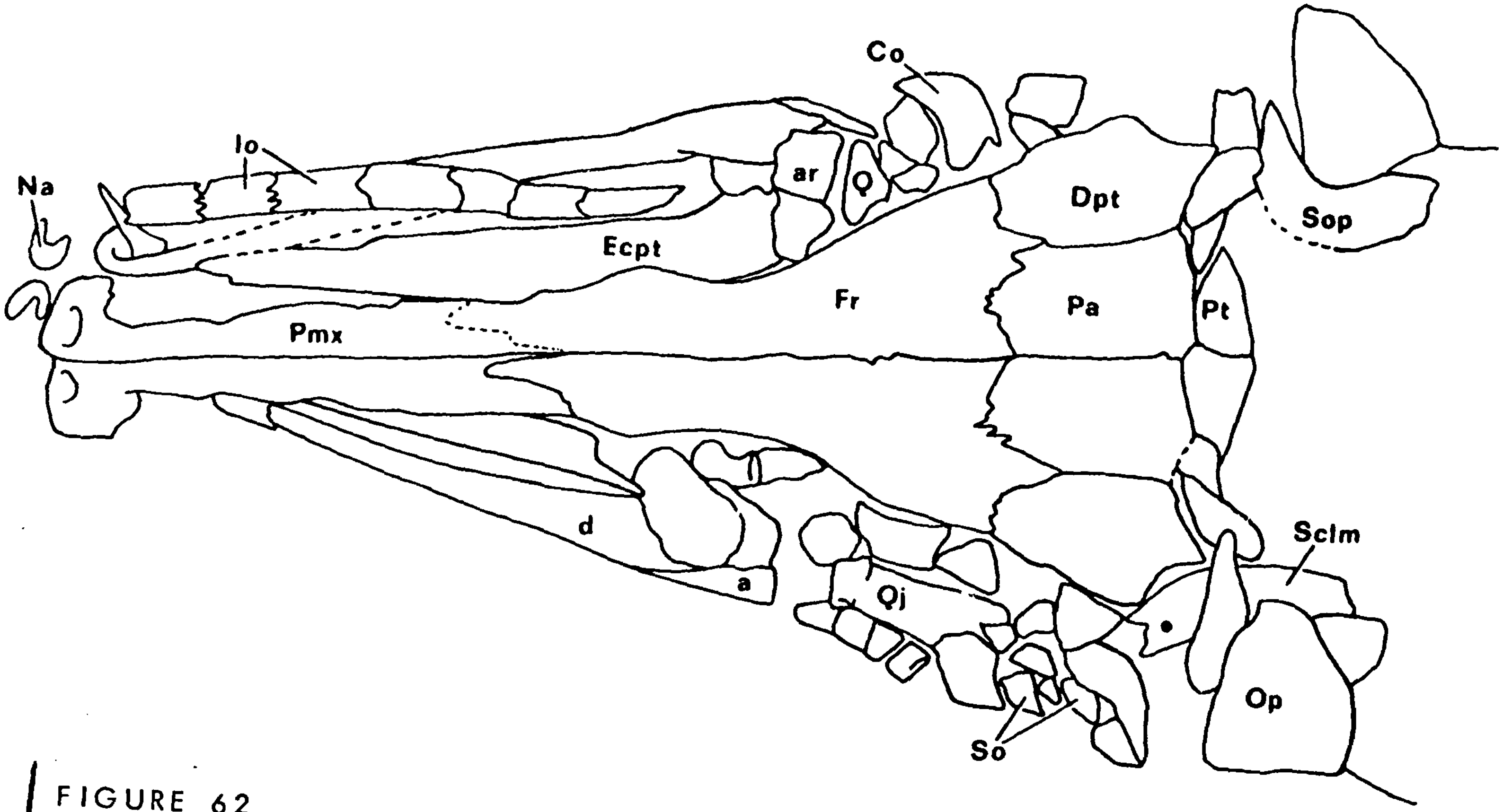

FIGURE 62

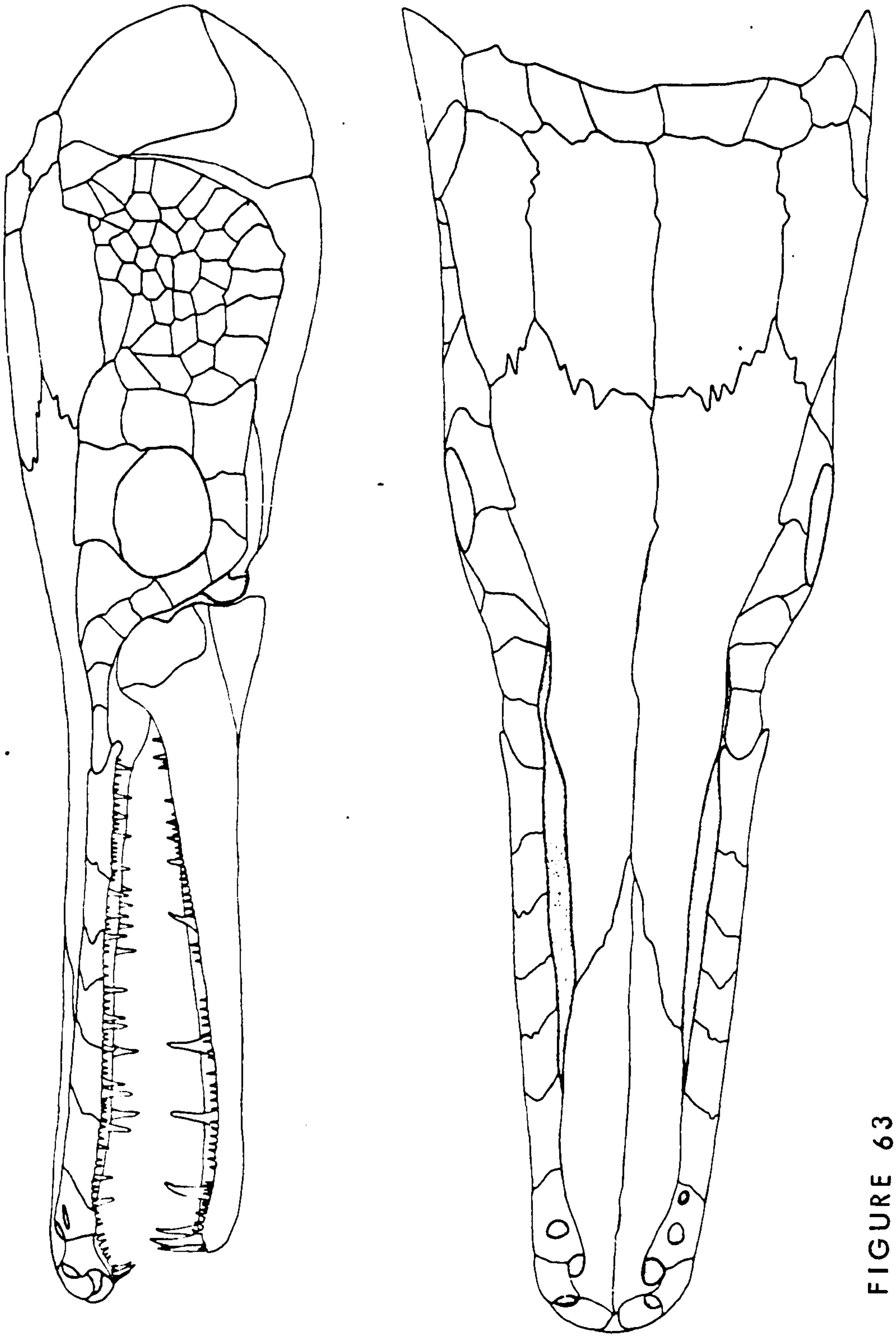

FIGURE 63

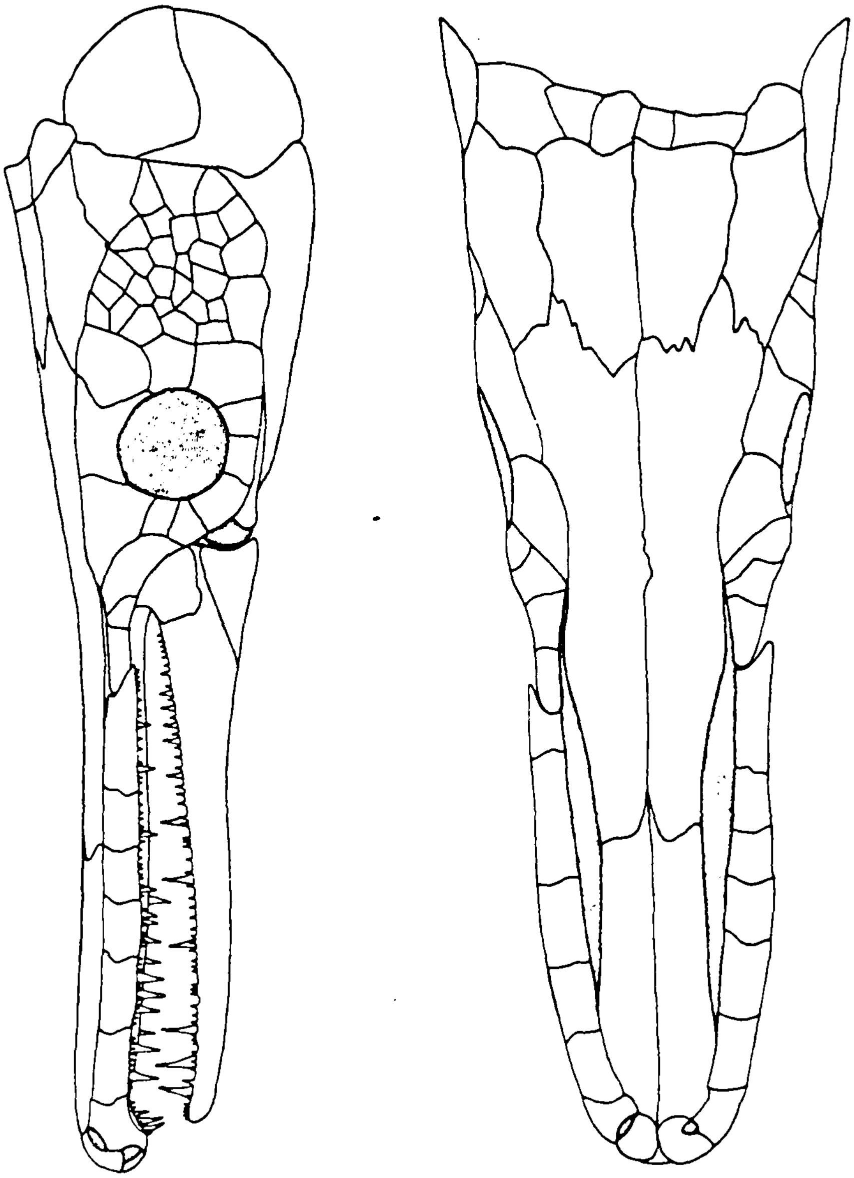

FIGURE 64

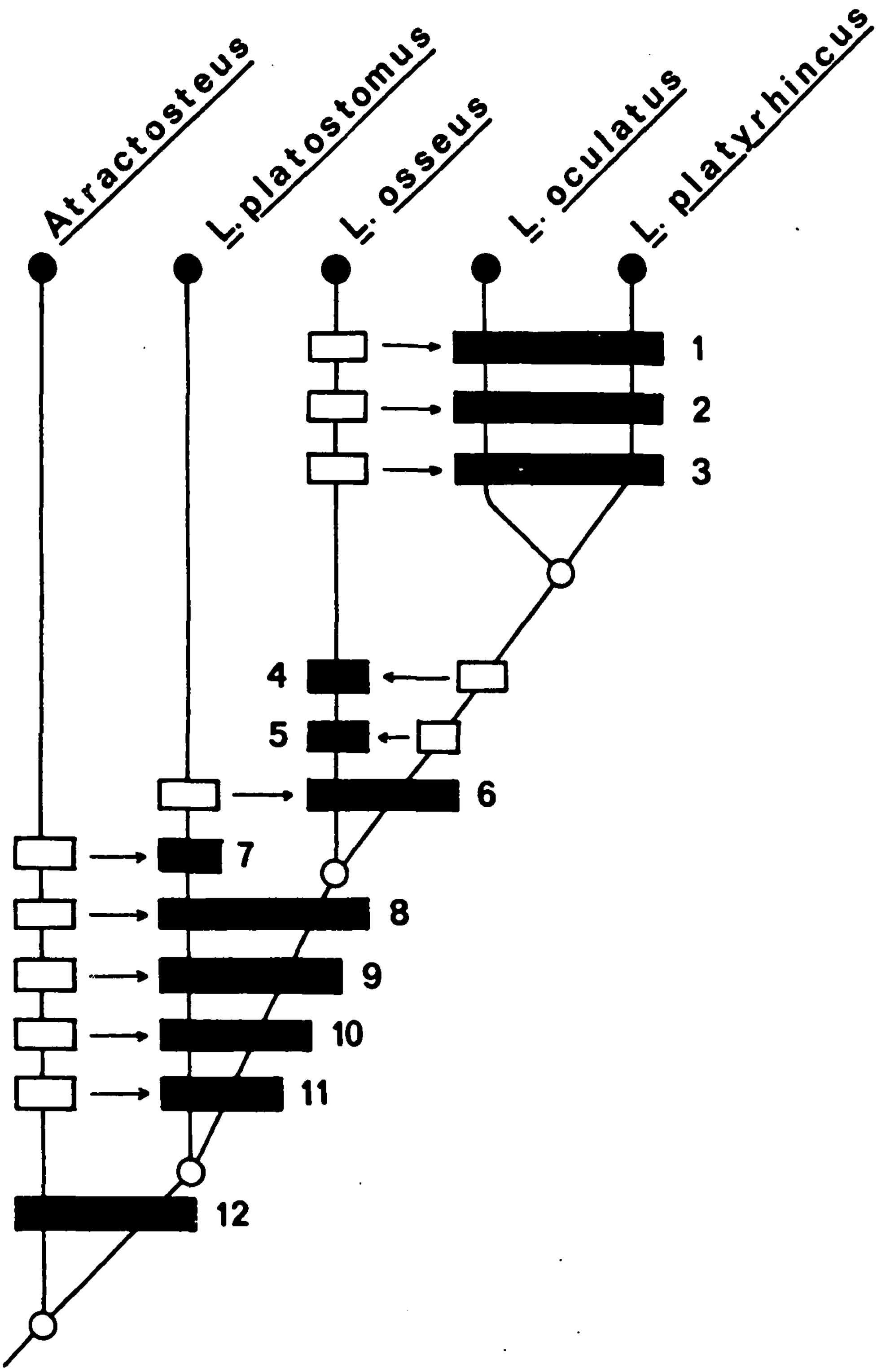
Atractosteus
L. platostomus
L. osseus
L. oculatus
L. platyrhincus
1
2
3
4
5
6
7
8
9
10
11
12

FIGURE 65

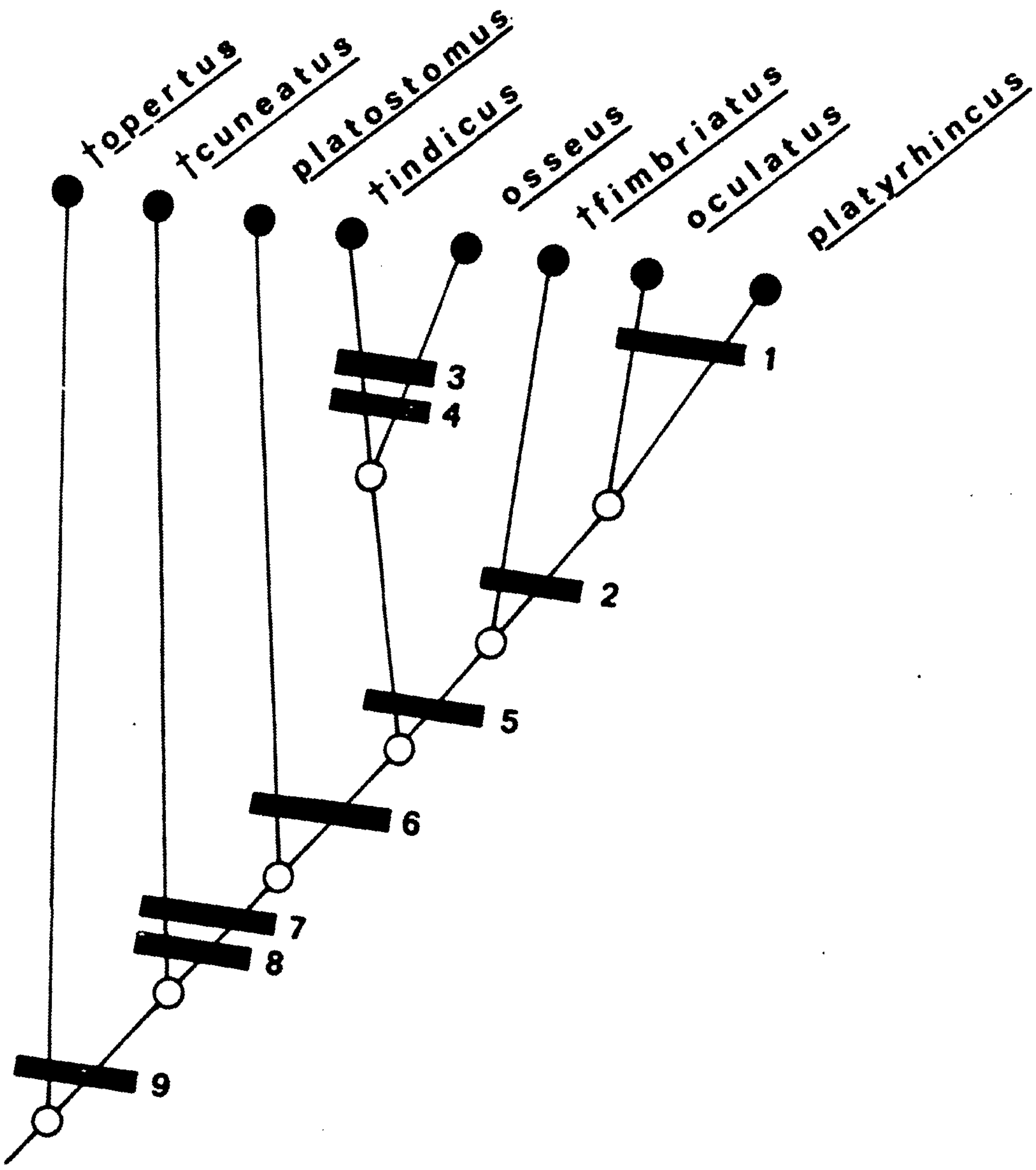
†opertus
†cuneatus
platostomus
†indicus
osseus
†fimbriatus
oculatus
platyrhincus
1
2
3
4
5
6
7
8
9

FIGURE 66

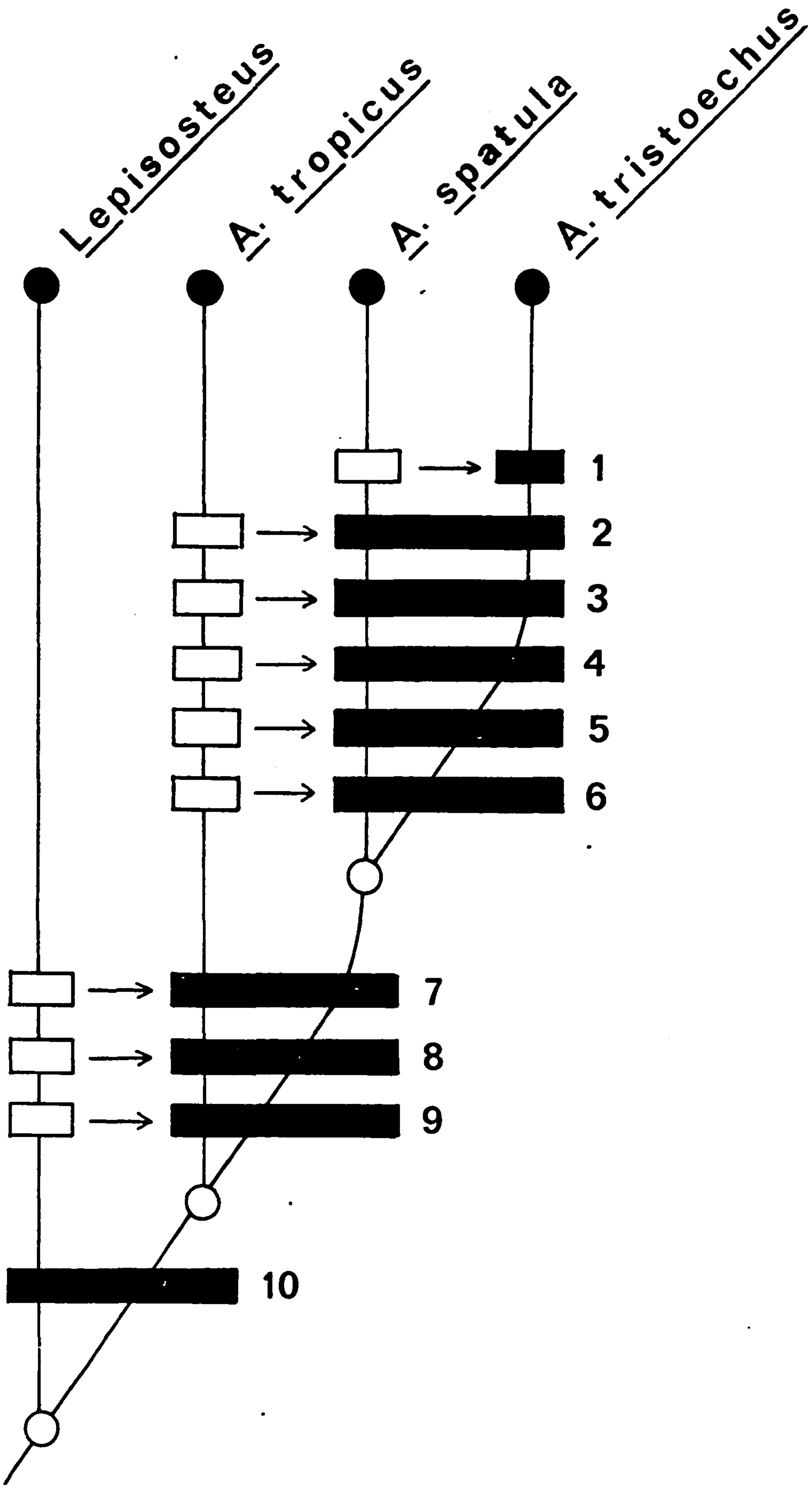
Lepisosteus
A. tropicus
A. spatula
A. tristoechus
1
2
3
4
5
6
7
8
9
10

FIGURE 67

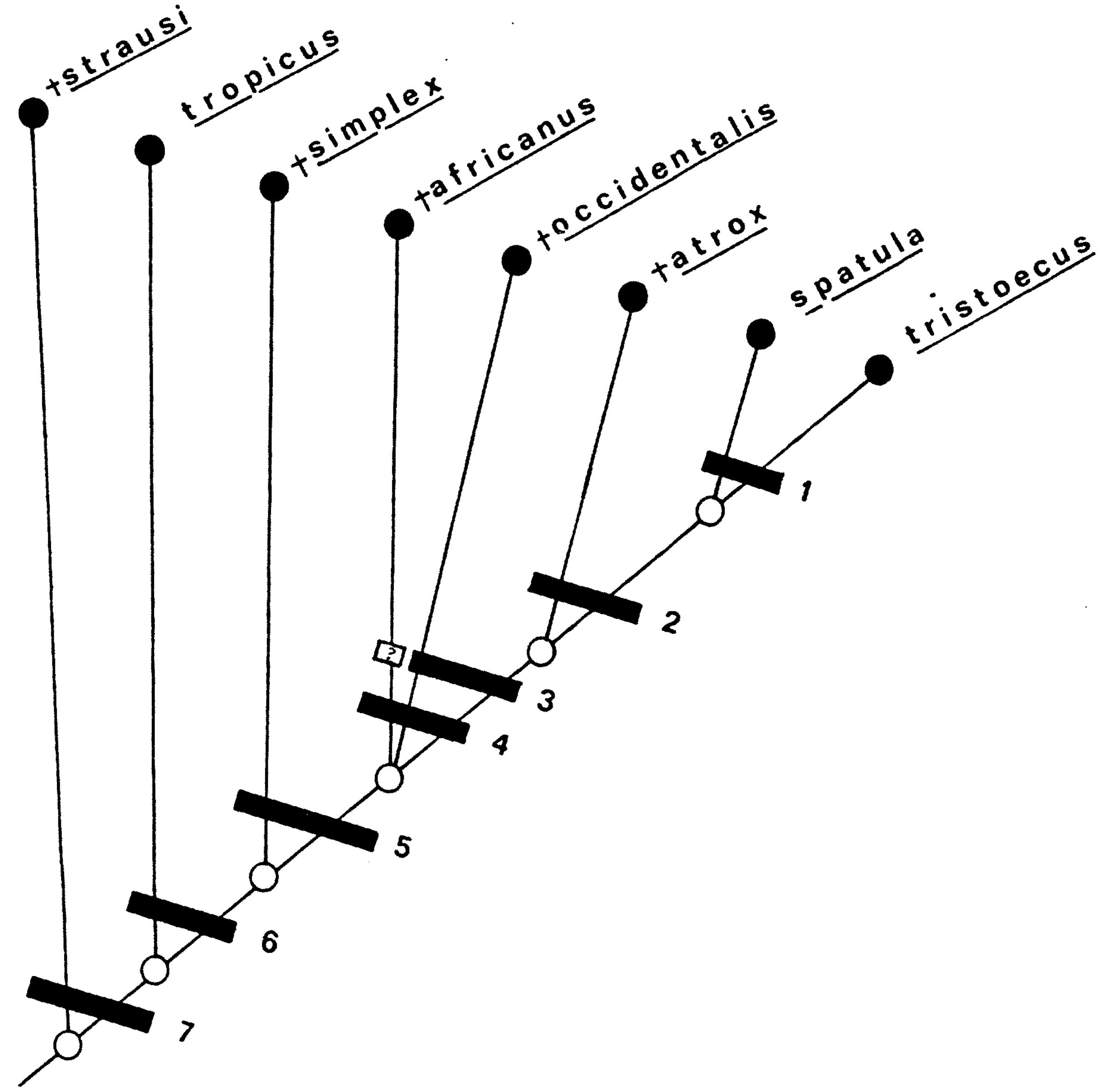
†strausi
tropicus
†simplex
†africanus
†occidentalis
†atrox
spatula
tristoecus
1
2
?
3
4
5
6
7

FIGURE 68

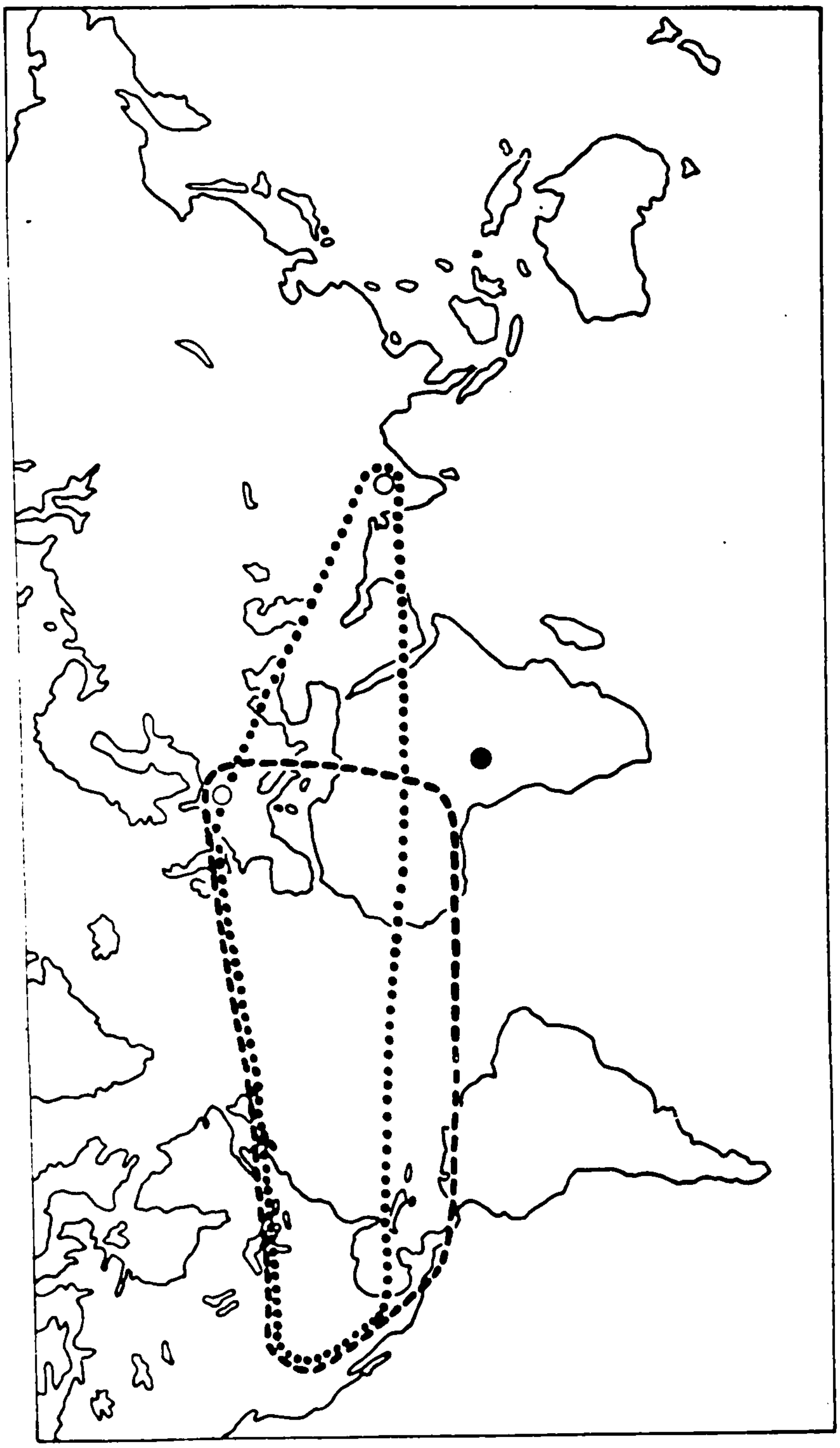

FIGURE 69

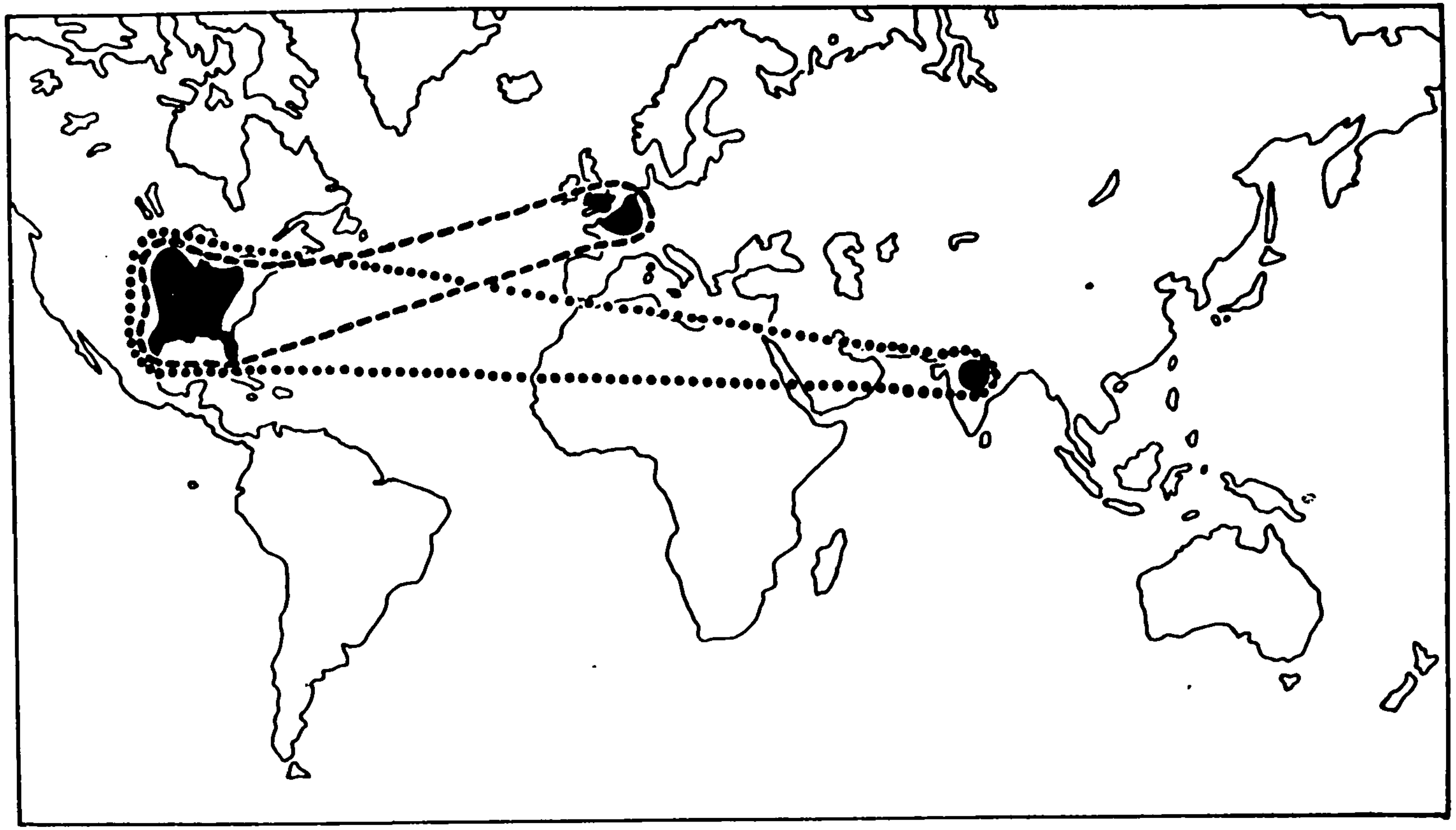

FIGURE 70

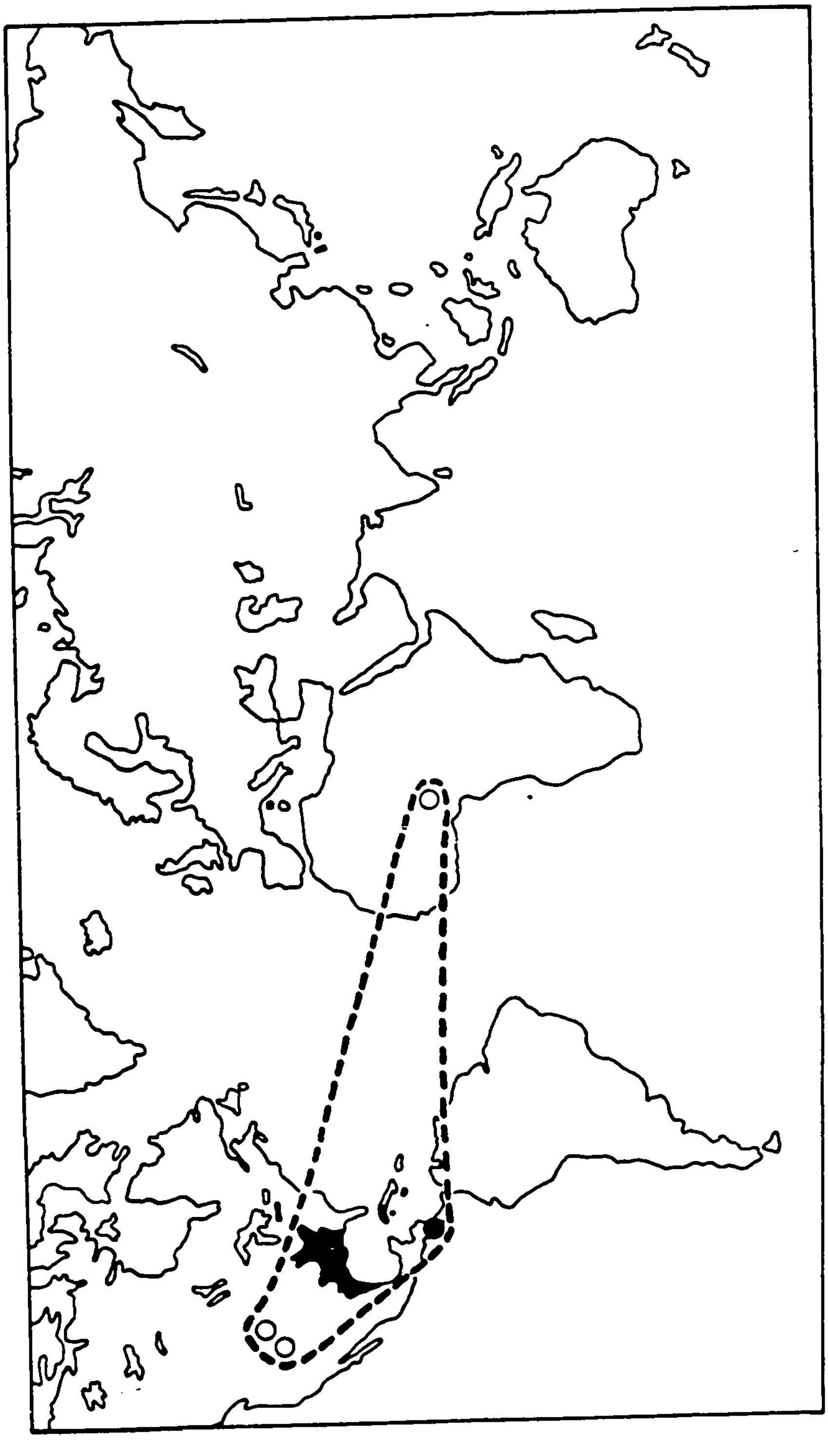

FIGURE 71

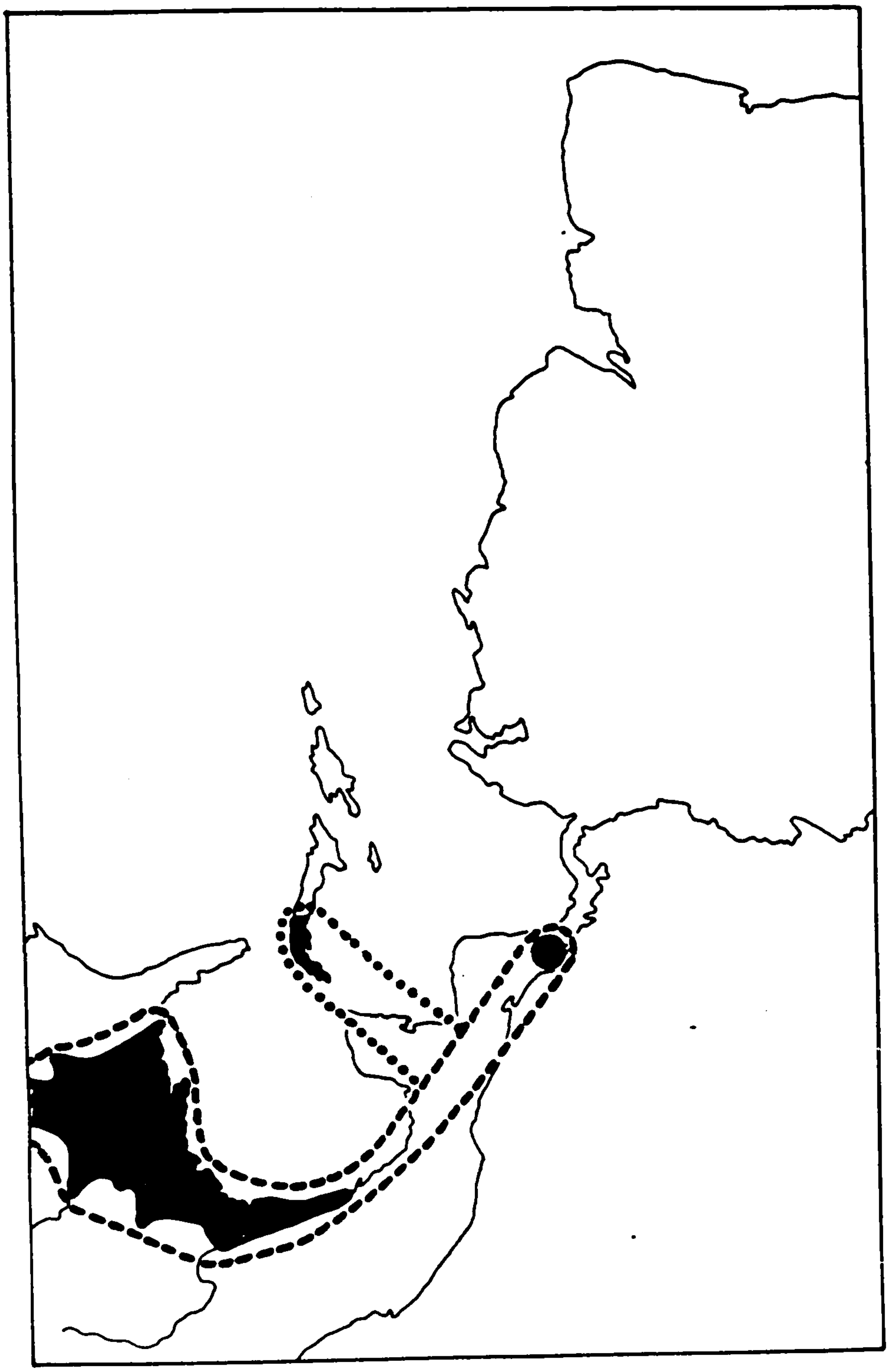

FIGURE 72