

CRETACEOUS AND TERTIARY
ACTINOPTERYGIAN FISHES
FROM BRAZIL

BOBB SCHAEFFER

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CONTENTS

INTRODUCTION	7
GEOLOGIC OCCURRENCE	8
SYSTEMATIC DESCRIPTIONS	12
Order Semionotoidea	12
Family Semionotidae	12
<i>Lepidotus</i> Agassiz	12
<i>Lepidotus piauihyensis</i> Roxo and Löfgren	12
Order Isospondyli	13
Suborder Clupeoidea	13
Family Leptolepidae	13
<i>Leptolepis</i> Agassiz	13
<i>Leptolepis bahiaensis</i> , new species	13
Family ?Elopidae	14
<i>Lastroichthys</i> , new genus	14
<i>Lastroichthys longipectoralis</i> , new species	14
Family Chirocentridae	15
<i>Chiromystus</i> Cope	15
<i>Chiromystus mawsoni</i> Cope	15
<i>Chiromystus alagoensis</i> Jordan	15
Family Chanidae	16
<i>Dastilbe</i> Jordan	16
<i>Dastilbe crandalli</i> Jordan	16
Family Clupeidae	17
<i>Knighia</i> Jordan	17
<i>Knighia branneri</i> (Jordan)	17
<i>Diplomystus</i> Cope	20
<i>Diplomystus longicostatus</i> Cope	20
Preliminary Analysis of the Double-armored Clupeids	21
Order Ostariophysi	24
Suborder Cyprinoidea	24
Family Characinidae	24
<i>Eobrycon</i> Jordan	24
<i>Eobrycon avus</i> (Woodward)	24
<i>Eobrycon branneri</i> Eigenmann	25
<i>Eobrycon ligniticus</i> (Woodward)	25
Order Acanthopterygii	28
Suborder Percoidea	28
Family Serranidae	28
<i>Percichthys</i> Girard	28
<i>Percichthys antiquus</i> Woodward	28
Family Cichlidae	29
<i>Aequidens</i> Eigenmann and Bray	29
<i>Aequidens pauloensis</i> , new species	29
DISCUSSION	30
Analysis of Fossil Assemblage	30
The Origin of the South American Fresh-water Fish Fauna	30
Marine Distribution	33
Land Bridge Dispersal	34
Distribution and Continental Drift	35
Holarctic Continental Distribution	35
REFERENCES	36

INTRODUCTION

FISHES FROM THE CRETACEOUS OF BRAZIL were first recorded by Spix and Martius in 1828. Since that time collections of Cretaceous and Tertiary actinopterygian fishes from various localities have been described by Agassiz, Cope, Woodward, Jordan, Maury, and Roxo.

The collection that forms the basis for this study was sent to the American Museum of Natural History in 1931 by Dr. Euzebio de Oliveira, former Director of the Geological Survey of Brazil. It includes material from localities in the States of São Paulo, Alagoas, Piauí, Baía, and Sergipe. Dr. Louis Hussakof partially examined this collection at the time of its reception and made some preliminary identifications, but unfortunately circumstances prevented a detailed study until undertaken by the present writer. Excepting the absence of material from the rather famous localities of the Série Araripe, Ceará, this collection is representative of most of the well-known localities. In addition, undescribed material from several new localities is herein included.

A satisfactory study of fossil fishes is limited to a great degree by the usual rather poor preservation of the material. Fossilization, such as occurs in the Green River and Mount Lebanon shales and certain localities in Europe, is exceptional, but highly desirable not only for morphological but also for quantitative studies. Very often important diagnostic skeletal characters are irretrievably smashed or obscured during preservation and, as is well known, dissociated fish remains are far more common than complete or partially complete skeletons. This situation has naturally led to differences of opinion in identification and certainly to an extreme state of taxonomic inflation in many groups, such as in the genus *Lepidotus*, with over 90 described species. Failure to compare new material with the genotype has also led to much confusion, as formerly existed in the case of the actinistian *Coelacanthus*. These problems are all too evident to anyone who has worked with fossil fishes and are here mentioned merely to emphasize certain inherent difficulties in dealing with this type of material, particularly in connection with evo-

lutionary and zoogeographical studies. Until critical analyses, based on most of the known available material, are made, particularly of certain genera with many species, such as *Lepidotus*, it would appear that a conservative approach, at least towards the creation of additional related genera, is advisable. The designation of new species based on slight and possibly statistically invalid differences seems inevitable, however, unless critical studies are possible and the range of variation within such species is determined. A similar situation exists for the genus *Leptolepis*, as noted by Dunkle (1942, p. 64) and confirmed by the present writer. In this case it may prove necessary to revise the entire family Leptolepididae.

The problem of the origin of the Recent South American fresh-water fish fauna is still unsolved. An attempt is made in the discussion, however, to evaluate the evidence presented by the fresh-water fossil fishes thus far discovered in Brazil. It is obvious that this question will require far more fossil evidence for a solution as satisfactory as that obtained for the origin of the Tertiary mammalian fauna of South America.

The writer wishes to acknowledge his gratitude to Dr. W. K. Gregory, Dr. G. G. Simpson, Dr. C. M. Breder, Jr., and Dr. E. H. Colbert for critically reading the manuscript and for helpful suggestions. He is also indebted to Mr. J. T. Nichols for assistance in certain problems related to recent ichthyology and to Dr. L. I. Price of the Division of Geology and Mineralogy, Ministry of Agriculture, Brazil, for information on the geology and the collecting localities. Dr. M. de Oliveira Roxo, Director of the Division of Geology and Mineralogy, very kindly supplied several useful maps. The author is obligated to Mr. J. Le Roy Kay for the loan of specimens from the Carnegie Museum.

The following abbreviations have been used in referring to catalogued specimens:

A.M.N.H., American Museum of Natural History
B.M.N.H., British Museum (Natural History)
C.M., Carnegie Museum
Col. Pad. Serv. Geol. Min., Collecção Padrão do Serviço Geológico e Mineralógico of Brazil

GEOLOGIC OCCURRENCE

TABLE 1 represents an attempt to assign a definite age to most of the localities in Brazil from which fossil fish have been obtained. It is based mainly on the recent work of Maury (1930, 1936), E. P. de Oliveira (1939), and A. I. de Oliveira and Leonardos (1943). The last-named work has been particularly helpful in that it represents a synthesis of most of the work accomplished since early in the last century. There is still some difference of opinion regarding the age of several of the localities and formations, and it is un-

fortunate that the fish fauna cannot be reliably used for making definite determinations.

The Lower Cretaceous is represented by deposits in the States of Pernambuco, Sergipe, Baía, and Rio Grande Do Norte. The Série Baía extending northward from Baía de Todos os Santos, and the Formação Almada, a localized deposit north of Ilhéus, Baía, were formerly placed in the Lower Cretaceous. Roxo (1936) considers the Série Baía to be Upper Cretaceous on a faunistic

TABLE 1

Period or Epoch		Stage	Locality	Nature of Sediments
Tertiary	?Pliocene	Unknown	Taubaté and Tremembé, São Paulo	Shale, lacustrine-fluvial
		Unknown	Nova York, Maranhão	Shale, probably lacustrine-fluvial
	?Lower Eocene	Sparnacian or Thanetian	Formação Maria Farinha, Pernambuco	Limestone, marine
			Série Alagaos in vicinity of Riacho Doce, Alagaos	Bituminous shale, estuarine
Cretaceous	Upper	Maestrichtian	Rio Gramame Limestone, Paraíba	Limestone, marine
		?Senonian (formerly considered Lower Neocomian)	Série Baía exposed along eastern shore of Baía de Todos os Santos	Shales and sandstones, estuarine
			Fomação Almada, Baía	Shale, estuarine
		Turonian or Cenomanian	Série Araripe a. Formação Santana, Ceará	Concretions in sandstone and limestone, marine
			(Série Grajaú) b. Isolated deposit, east of Floriano, Piauí	Limestone, marine
			c. Barra do Corda, Maranhão	?
	Lower	Middle or Upper Albian	Lastro Oolitic Limestone (Série Sergipe, Grupo Ganhamaroba), Rio Ganhamaroba, Sergipe	Oolitic limestone, marine

basis, and a copy of the "Atlas Geológico Do Brasil" (E. P. de Oliveira, 1939) recently received has been annotated by Dr. M. J. de Oliveira Roxo, placing both the Série Baía and the Formação Almada in the Upper Cretaceous (? Senonian). This determination is more in agreement with the Upper Cretaceous nature of the fish fauna, particularly with the presence of a diplomystid and an amiid. The Série Baía is an estuarine deposit of shales and sandstones and has been described most completely by Woodward and Mawson (1907). Most of the fossil fishes from this series have actually been found in the shales exposed along the eastern shore of the bay, north of the city of Salvador. The Formação Almada has produced lepidotid remains and a single species of clupeid.

The Grupo Ganhamaroba, more specifically the Lastro Oolitic Limestone of the Série Sergipe, has yielded several specimens from beds exposed along the Rio Ganhamaroba, a branch of the Rio Sergipe. This deposit is considered to be Middle or Upper Albian and, with the assignment of the Série Baía and Formação Almada to the Upper Cretaceous, this is the only recorded Lower Cretaceous deposit containing fish remains.

The Upper Cretaceous deposits are relatively very extensive, particularly in Maranhão, western Baía, and Matto Grosso, with smaller exposures in Ceará, Rio Grande Do Norte, Minas Gerais, and Goyaz. The richest fossil fish fauna and probably the best known is that from various localities in the Formação Santana of the Série Araripe, Ceará. This is a marine formation considered to be Turonian and consisting of shales and sandstones with the fossils occurring in concretions which are found for the most part in the shales. While Spix and Martius first reported fossils from here in their "Reise in Brasilien" published in 1828, the most complete studies of the fauna are those of Jordan (1908 and 1921). The most distinctive feature of the Série Araripe is the large preponderance of elopids, a group probably represented in but one other known Brazilian locality.

Upper Cretaceous beds near Floriano, Piauí, and Barra do Corda, Maranhão, have yielded a small amount of material, the latter

showing faunal relationships with the Série Araripe (Rego, 1923).

The Rio Gramame Limestone, considered to be Maestrichtian (Maury, 1930), is represented by an isolated deposit in eastern Paraíba. From it have been obtained a pycnodontid and a stomiatoid.

The Série Alagoas is generally considered to be an Eocene estuarine deposit consisting of bituminous shales. It is exposed along the coast of Alagoas, in some places only at low tide, at about six localities from a point south of Maceió northward to Maragogi and is overlain by thick beds of probably Miocene-Pliocene age. The only locality that has yielded a fossil fish fauna is the village of Riacho Doce, described by Jordan (1910).

The Formação Maria Farinha, consisting of a series of localized marine limestones along the coast of Pernambuco, is considered to be basal Eocene, equivalent to the Midway group of Texas by Maury (1930, p. 33). Oliveira and Leonardos (1943, p. 425) consider the formation to be Upper Cretaceous (Danian), but do state that it may be Paleocene (*op. cit.*, p. 622). It is considered as basal Eocene in the table. A fragment of a stomiatoid was described by Cope from this formation.

A lacustrine-fluvial deposit of unknown Tertiary age is present in the southeastern portion of São Paulo. Two localities, near the towns of Taubaté and Tremembé, have yielded a small fauna first described by Woodward in 1898. Woodward (1939) has described two fossil fishes from an unrecorded Tertiary formation at Nova York on the Rio Parnaíba in Maranhão, and he believes the fossils indicate early Tertiary age, possibly Eocene.

The wide separation of fossiliferous localities of similar age would seem to indicate that the actinopterygian fauna, as it is now known, represents but a small sample of the material that might be obtained with more intensive collecting. As will be discussed later, fossil fishes from fresh-water deposits, in particular, are of primary importance in throwing some light on the unsolved problem of the dispersal of the Recent South American fresh-water fishes. The fauna thus far discovered unfortunately offers little more than a few tantalizing suggestions on this problem.

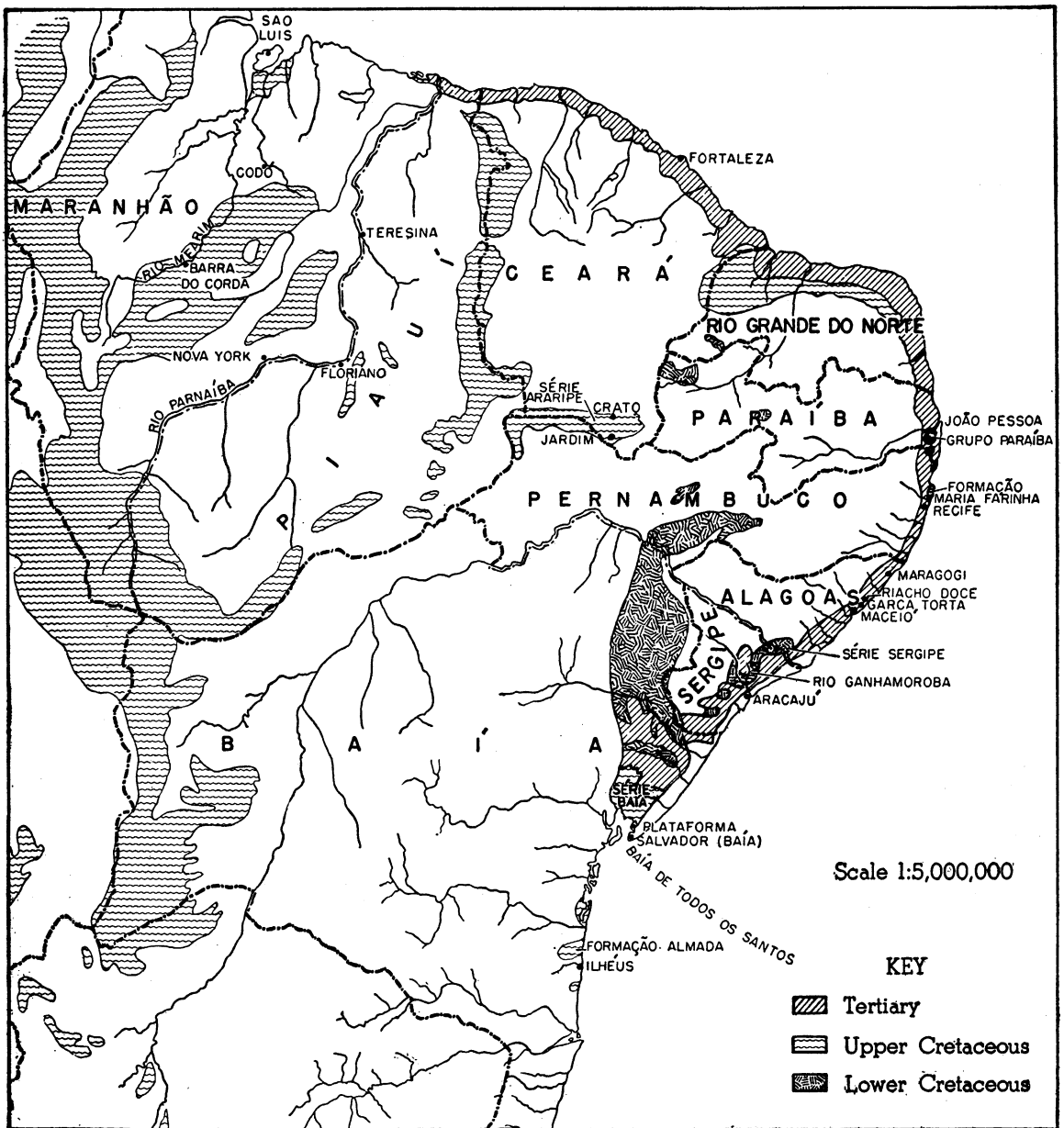


FIG. 1. Map of northeastern Brazil showing the Cretaceous and Tertiary deposits and localities from which fossil fishes have been obtained. This map is based on the Geological Map of South America published by the Geological Society of America (1945) and on various other sources mentioned in the text.

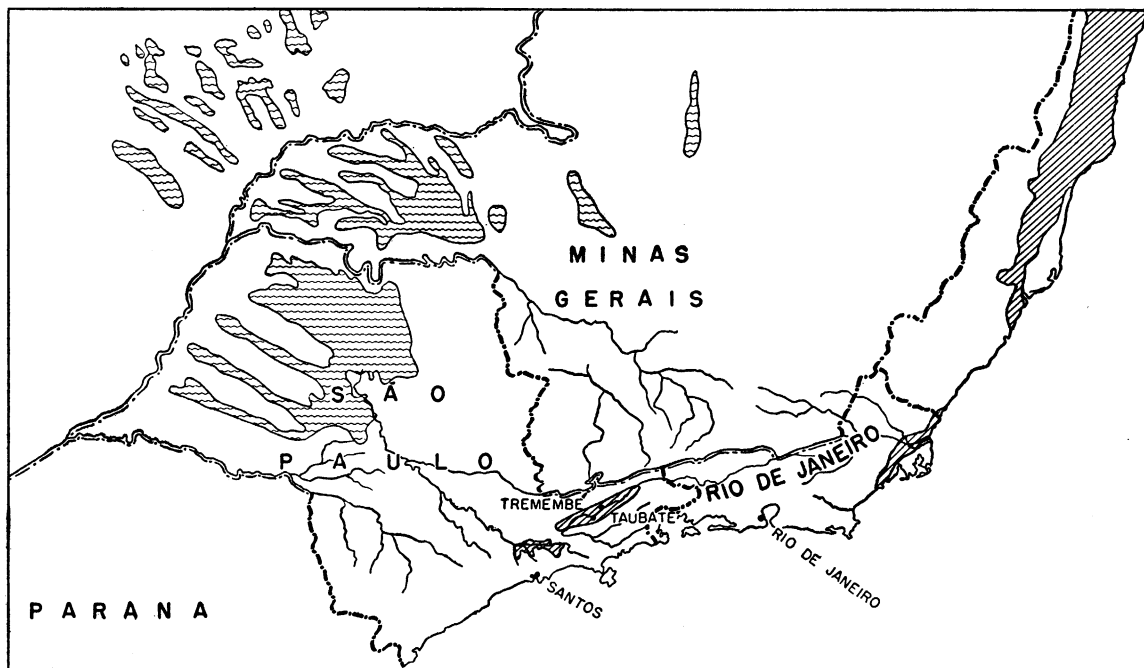


FIG. 2. Map of São Paulo and adjacent states to show particularly the Tertiary deposits around Tremembé and Taubaté. The scale, key, and sources of this map are the same as in figure 1.

SYSTEMATIC DESCRIPTIONS

ORDER SEMIONOTOIDEA

FAMILY SEMIONOTIDAE

GENUS *LEPIDOTUS* AGASSIZ, 1832

(For generic synonymy and generic diagnosis, see Woodward, 1895, p. 77.)

GENOTYPE: *Lepidotus elvensis* (De Blainville).

Lepidotus piauihyensis Roxo and Löfgren, 1936

Lepidotus piauihyensis ROXO AND LÖFGREN, 1936, p. 7, figs. 1, 2.

Lepidotus piauihyensis, SANTOS, 1945, p. 1, pls. 1-4.

TYPE: Col. Pad. Serv. Geol. Min. No. 3447. Complete fish excepting imperfectly preserved fins.

HORIZON AND LOCALITY: Série Araripe (Grajau), Formação Santana, Upper Cretaceous, near Floriano, Piauí.

REVISED DIAGNOSIS: Length about 56 cm., greatest depth 20 cm. Head about one-quarter total body length. Dorsal outline elevated anterior to dorsal fin. Dermal bones of skull tuberculated, distribution and concentration of tubercles not constant. Parietals about one-third length of frontals, maximum width of opercular somewhat more than one-half greatest length. Scales smooth, without ornamentation in any region of body. Scale enamel usually lacking in some areas. Dorsal 9, pectoral 12, pelvic 8-9, anal 8. Origin of dorsal fin about halfway between origin of pectoral and origin of anal fins.

REMARKS: The two specimens of *Lepidotus piauihyensis* in the present collection, A.M. N.H. No. 10012 and A.M.N.H. No. 10013, were obtained in 1913 from a locality near Riacho Olhos d'Agua, Floriano, Piauí. The type description is based on a third specimen found between the towns of Amarante and Floriano on the right bank of the Rio Parnaíba. The latter specimen is deposited in the collection of the Serviço Geológico e Mineralógico, Brazil.

Lepidotus (pl. 1, fig. 1) is obviously distinct from the three previously described species of the Brazilian Cretaceous, although it does share certain characters in common with several European forms. The dermal elements of the skull have been studied by

Santos (1945). They agree in relative size and arrangement with the typical lepidotid condition as described by Dechaseau (1943) for *L. elvensis*. There appears to be a reduction, however, in the number of postorbitals with a single element under the eye rather than a series of four or five.

Lepidotus temnurus, described by Agassiz (1841) from the Série Araripe, has scales that are characteristically marked with three coarse ridges, and the lateral line scales are distinctly elevated. *Lepidotus mawsoni* was founded by Woodward (1888) on detached fragments from the Série Baía. The scales show occasional faint posterior radiating grooves with some crenulations but are otherwise smooth. They are considered to be unusual in the great thickness of the laminated bony base, but unfortunately no measurements of this layer are given to make comparison possible. The bony layer of the scales of *L. piauihyensis* in cross section appears to be of a thickness characteristic of the genus. *L. piauihyensis* resembles *L. mawsoni* in the presence of discontinuous enamel in the flank-scale area and in the development of peculiar rounded excrescences, possibly developed from the bony base of the scale, although this cannot be demonstrated in ground sections. One specimen in this collection (pl. 1, fig. 1) has two such protuberances in the flank area.

Lepidotus souzai was described by Woodward (1908) from beds probably referable to the Formação Almada. The bones of the skull are tuberculated as in *L. piauihyensis*, but the scales are covered with thickened enamel and have six to eight radiating furrows. The ridges between the furrows are covered with tubercles. *L. souzai* and *L. piauihyensis* are both short and relatively stout species and in this respect resemble *L. mantelli* from the Lower Cretaceous of Europe. Weiler (1935) considers a lepidotid from the Upper Cretaceous of Egypt to have an affinity with *L. souzai* because of similar scale characters.

There is thus reasonably good evidence, based mainly on distinctive scale characters, that four species of *Lepidotus* occur in the Cretaceous formations of Brazil. Of the four

species described from North America, scale characters are again relied upon almost entirely and usually through necessity. Eastman (1917), for instance, compared *L. walcotti* from the Kiowa Shales of Kansas with *L. gallineki* from the Rheatic of Upper Silesia with which he considered it to be closely related, presumably on the basis of scale morphology. There is a very close resemblance between the scales of *L. piauihyensis* and those of *L. congolensis* Hussakof (1917) from the possibly Upper Triassic Lualaba Beds of the Belgian Congo, and, for that matter, with several of the North American and European species.

Many of the 90 odd described species of this world-wide genus are based on scale characters alone, and it is very tempting to see genetic affinities in species with similar scale morphology. While it is true that scale characters may turn out to be as constant and reliable in the Holostei as they appear to be in the Teleostei on the basis of the work of Cockerell and David, the significance of close similarity, for instance in *Lepidotus*, between the scales of species from widely separated regions and from different ages is yet to be determined. The role played by parallelism is, for instance, unknown.

The key worked out by Woodward (1895, p. 82) for about 16 species of *Lepidotus* involves the relative length of the frontals and parietals, relation between breadth and depth of the opercular, tooth form and scale morphology. Unfortunately, such a key cannot be developed for a majority of the species, as information on most of these characters is not available.

ORDER ISOSPONDYLI

SUBORDER CLUPEOIDEA

FAMILY LEPTOLEPIDAE

GENUS LEPTOLEPIS AGASSIZ, 1832

(For generic synonymy and generic diagnosis, see Woodward, 1895, p. 501).

GENOTYPE: *Leptolepis coryphaenoides* (Bronn).

Leptolepis bahiaensis,¹ new species

¹ From Bahia (also spelled Bafa), the state in which the specimens were found.

TYPE: A.M.N.H. No. 10014. Complete fish with somewhat imperfect fins.

HORIZON AND LOCALITY: ?Serie Baía, Upper Cretaceous, Bacuparytuba, Baía. (Exact location of Bacuparytuba unknown to Brazilian Survey.)

SPECIFIC DIAGNOSIS: Fish of small size, ranging between 4.4 and 5.7 cm. in length. Head somewhat less than one-quarter total length of body. Origin of pelvic fin opposite origin of dorsal fin, origin of anal fin halfway between origin of pelvic and origin of caudal fins. Vertebrae about 38, of which approximately 15 are caudal. Maxillary a wide curved plate, dentary of characteristic shape with robust coronoid process.

REMARKS: This is the first record of *Leptolepis* from Brazil, excepting an otolith from the Série Araripe considered to be leptolepid by Erasmo (1938). *L. australis* has been described from Argentina (De Saez, 1939), representing apparently the one other described species from South America.

The skull of *L. bahiaensis* (pl. 2, fig. 2) appears to conform closely to the typical leptolepid pattern. The premaxillary is characteristically small, apparently represented by an enlarged area at the distal end of the maxillary. The supramaxillaries are not well preserved and cannot be properly distinguished from each other or from the maxillary. Dermal elements of the upper jaw as a whole resemble closely those found in *L. sprattiformis* from the Upper Triassic of Solenhofen.

The circumorbital series is missing in the type, revealing a rather badly crushed palatal complex that resembles very closely Rayner's restoration (1937) of this region in the genotype *L. coryphaenoides*. The articulation between the quadrate and articular is clearly defined, indicating a suspensorium swung forward to about the same degree as in the genotype. The opercular elements are also somewhat crushed but appear to be typical in relative size and arrangement.

About four branchiostegal rays are present below the ventral margin of the opercular region, and are typically broad and flat. A portion of the left hyoid arch is preserved. The distal ossification of the ceratohyal appears to be hourglass-shaped with possibly a

bar of bone running between the proximal and distal portions along the dorsal border as in *L. coryphaenoides*.

Most of the dermal portion of the pectoral girdle is preserved, but separate elements cannot be recognized. The cleithrum has a rather prominent longitudinal ridge as in the genotype, while the posterior expansion at the lower end is relatively greater than in the genotype and the anterior expansion relatively smaller.

The postcranial skeleton (pl. 2, fig. 1) is quite typical. The vertebrae are well ossified cylinders with two lateral, longitudinal laminae. The notochordal canal is relatively large and easily demonstrated in hemisected vertebrae. The neural arches are delicate and attenuated with intermuscular bones lying across them anteriorly. The dual nature of the former cannot be satisfactorily demonstrated. The ribs are moderately robust with a longitudinal groove on the lateral side.

The relative positions of the fins have been indicated in the diagnosis. The dorsal has about 10–12 rays, pectoral 12, pelvic about 9, and anal about 9. The pelvic girdle appears to be an elongated and exceedingly thin plate which makes it very difficult to uncover satisfactorily. The hypural elements of the caudal fin appear to be less expanded than those of *L. coryphaenoides* and more like those in *L. voithi* or *L. dubius*. The detailed structure of the caudal fin is not clearly demonstrated in any of the specimens, but it is evident that the homocercal condition is being approached as in *L. nevadensis* (David, 1941). There are but five or six vertebrae contributing to the structure of the tail. There is no evidence of the ray-like fulcral scales along the dorsal border of the epaxial lobe of the caudal as in the genotype.

The genus *Tharrhias* was established by Jordan and Branner (1908) for a leptolepid from the Série Araripe. It is distinguished from *Leptolepis* by having a relatively larger operculum, which is four times deeper than the suboperculum, a greater number of vertebrae, and by a larger body size. *Haplospondylus*, a Lower Cretaceous leptolepid from Argentina (Cabrera, 1927), appears to resemble *Tharrhias* more closely in the opercular region, although Erasmo (1938) considers it to be possibly synonymous with

Leptolepis on the basis of resemblance in the vertebrae and dentary. Although leptolepids have been reported from Cuba and Mexico, the remains thus far described are too fragmentary for comparison.

Leptolepis schoewei Dunkle (1942), from the probable Upper Triassic of Colorado, is a much more primitive type with an unconstricted notochord and ring-like centra. *L. nevadensis*, from the probable Lower Cretaceous of Nevada, is about the same size but has a larger number of vertebrae (50).

FAMILY ?ELOPIDAE

LASTROICHTHYS,¹ NEW GENUS

GENOTYPE: *Lastroichthys longipectoralis*, new species.

GENERIC DIAGNOSIS: Trunk relatively short, head approximately one-quarter total body length. Gape of mouth wide, extending behind orbit. Sclerotic ossified. Suspensorium vertical. Suborbital region wide. Centra cuboidal, constricted, with single lateral lamina. Neurapophyses and haemapophyses long and delicate. Anal extended.

Lastroichthys longipectoralis,² new species

TYPE: A.M.N.H. No. 10017. Incomplete fish with poorly preserved skull, dorsal fin and posterior portion of caudal region missing.

HORIZON AND LOCALITY: Lastro Oolitic limestone, Grupo Ganhamaroba, Série Sergipe, Lower Cretaceous, Rio Ganhamaroba, Sergipe.

SPECIFIC DIAGNOSIS: Length to end of caudal fin approximately 34 cm. Head about 12 cm. in length. Width of operculum about two-thirds of depth with tuberculated striations radiating from point of attachment. Articular with longitudinal striations. Total number of vertebrae unknown, abdominal about 18–20. Pectoral fin 14–15, pelvic fin about 10, anal approximately 25. Origin of dorsal fin midway between origin of pectoral fin and origin of pelvic fin. Pectoral fin inserted on ventral border and extending beyond origin of pelvic fin. Origin of pelvic fin midway between origins of pectoral and anal

¹ From Lastro, the name of the limestone deposit in which the specimen was found.

² In allusion to elongated pectoral fin.

fin. Pelvic rays extending to origin of anal fin. Extended anal fin with long rays.

REMARKS: Apparently *Lastroichthys* (pl. 1, fig. 2) is the second Cretaceous vertebrate to be discovered in the State of Sergipe, the other being *Palaeobalistum flabellatum* (Cope). The locality from which the latter was collected is unknown, but the horizon is probably Middle Albian (Maury, 1936) and possibly the same as that for *Lastroichthys*.

With diagnostic portions of the skeleton missing, it is difficult to determine the affinities of this new genus. The width of the area between the orbital region and the anterior border of the preopercular indicates that the suborbitals were large as in the Elopidae. The wide gape, probably small teeth, ossified sclerotic ring, and striated opercular further suggest association with the Elopidae, particularly with such forms as *Thrissopater* or *Pachyrhizodus* from the Upper Cretaceous. The elongated fins and rather delicate skeleton with thin dermal skull bones further suggest a tendency towards a deep-sea habitus, a trend likewise found to some extent in the elopids.

The vertebrae are not characteristically elopid, having constricted centra externally and a single lateral lamina. The typical elopid vertebrae do not have centra constricted externally and usually have two or three lateral fossae with intervening bars. The condition found in *Lastroichthys* resembles very closely that found in the Clupeidae, and on the basis of the vertebrae alone this genus might very reasonably be assigned to that family. The Cretaceous elopid *Pachyrhizodus* does have somewhat similar vertebrae, although the single lamina is much thicker.

Relationship with the Characinidae is possible in view of the evidence here presented favoring a Cretaceous marine habitus for this family. The enlarged suborbitals, elongated pectoral, extended anal, character of the vertebrae, and finally the wide gape are all present in this family. As these are not in themselves distinctive characin characters, it is not deemed advisable to refer *Lastroichthys* to this family. A more detailed knowledge of the skull must be available before assignment to the Characinidae could be considered.

There is likewise some resemblance to the

Enchodontidae and to certain of the Iniomi, but it appears to be based on such characters as those listed in the preceding paragraph, characters that are common to several suborders.

Lastroichthys longipectoralis is thus assigned tentatively to the Elopidae, until additional material makes a more detailed study possible.

FAMILY CHIROCENTRIDAE

GENUS CHIROMYSTUS COPE, 1885

Chiromystus COPE, 1885, p. 4.

GENOTYPE: *Chiromystus mawsoni* Cope.

REVISED GENERIC DIAGNOSIS: Trunk elongate as in other chirocentrids. Mouth large, oblique. Maxillary narrow, extending beyond posterior border of eye. Small styliiform teeth in shallow pockets on maxillary, premaxillary, and dentary; those at mandibular symphysis enlarged. Pectoral fin large, anterior rays broad and flat, pelvic and dorsal fins small, anal fin extended and lacking anterior acuminate lobe. Caudal fin deeply forked, lobes narrow, pointed at ends. Vertebrae with three prominent lateral laminae. Ribs moderately robust, with longitudinal groove. Scales cycloid, delicate.

Chiromystus mawsoni Cope, 1885

Chiromystus mawsoni COPE, 1885, p. 4.

Chiromystus mawsoni, WOODWARD, 1888, p. 134.

Chiromystus mawsoni, WOODWARD, 1901, p. 90.

Chiromystus mawsoni, ROXO, 1936, p. 67.

TYPE: Status unknown; should be in the American Museum of Natural History but cannot be located.

HORIZON AND LOCALITY: Série Baía, Upper Cretaceous, eastern shore of Baía de Todos os Santos, near Agua Comprida, Baía.

DIAGNOSIS: (Based on Cope and Woodward.) Length about 15–40 cm. Vertebrae 50: abdominal 28, caudal 22. Anal fin 16. Small dorsal opposing anal, origin of anal equidistant between pelvic and caudal.

Chiromystus alagoensis Jordan, 1910

Chiromystus alagoensis JORDAN, 1910, p. 32, pls. 12, 13.

TYPE: C. M. No. 5246/100. Almost complete skull and portion of pectoral fin.

HORIZON AND LOCALITY: Série Alagoas, ?Lower Eocene, near Riacho Doce, Alagoas.

REVISED SPECIFIC DIAGNOSIS: Length ranging from about 20 to 35 cm. Skull about one-fifth total body length. Vertebrae about 48: abdominal 21–23, caudal 25. Dorsal fin 16, pectoral fin 12, pelvic fin about 6, anal fin 21. Origin of dorsal fin opposite first third of anal fin, origin of pelvic midway between front of head and origin of caudal fin. Anal fin about equal to skull length.

REMARKS: Jordan (1910, p. 33) considered *C. alagoensis* (pl. 3, fig. 1) to differ from *C. mawsoni* (never figured) on the basis of a supposed difference in the relative size of the pelvic fin. In both species, however, this fin is "small," and no specific differences are indicated. There appears to be a smaller number of vertebrae in *C. alagoensis* and a larger number of anal rays. The known material for each species does not, however, permit an accurate count of the vertebrae. The size range is about the same as are also the observable details of the skull. Were it not for the difference in the age of the two species, it would be very reasonable to consider them synonymous, and this may prove desirable, particularly if the Série Alagoas proves to be Upper Cretaceous rather than Lower Tertiary.

The skull fragment, presumably *C. mawsoni*, figured by Allport (1860) appears to agree very closely with the type of *C. alagoensis*. Further preparation of the latter specimen (pl. 3, fig. 2) has revealed certain details of the skull not observed by Jordan, but they are unfortunately of little diagnostic value. The lacrimal is relatively large and the maxillary is relatively narrow as in *Chirocentrus* and in contrast to the condition found in *Portheus*. The supramaxillary and the circumorbital plates are relatively large, agreeing in this respect with *Ichthyodectes* and *Portheus*. The supraoccipital crest was apparently elevated as in the last-named genera.

The characters shared in common with *Platinx* from the Eocene of Europe include the small teeth set in close series, tendency towards enlargement of the pectoral fin, and lack of acuminate lobe on the anterior portion of the anal fin. It is very possible that *Chirocentrus* is related to this genus.

Cladocycclus gardneri Agassiz, a chirocentrid from the Série Araripe, differs from *Chirocentrus* in the position of the dorsal fin oppo-

site the pelvic. Were it not for this forward location of the dorsal, Woodward (1901, p. 108) would refer this genus, which may be world-wide, to *Ichthyodectes*.

REFERRED SPECIMENS: A.M.N.H. Nos. 10015, 10016.

FAMILY CHANIDAE

GENUS DASTILBE JORDAN, 1910

Dastilbe JORDAN, 1910, p. 29.

GENOTYPE: *Dastilbe crandalli* Jordan.

REVISED GENERIC DIAGNOSIS: Moderately elongate fishes with somewhat rounded ventral border. Dorsal and ventral scutes absent. Mouth small, oblique and jaws subequal. Opercular large, finely striated. Subopercular distinct, preopercular not expanded. Vertebral centrum with small notochordal canal, hourglass-shaped. Caudal portion of vertebral column of stegourous type with last vertebra elongated into a urostyle. Ribs short and with wide shallow groove on outer surface.

Dastilbe crandalli Jordan, 1910

Dastilbe crandalli JORDAN, 1910, p. 30, pl. 10, fig. 9.

TYPE: C. M. No. 5247/91. Complete fish with head imperfectly preserved.

HORIZON AND LOCALITY: Série Alagoas, ?Lower Eocene, Riacho Doce, Alagoas.

REVISED SPECIFIC DIAGNOSIS: Length ranging from 3.50 to 9.40 cm., greatest depth from 0.40 to 1.60 cm. Head one-quarter to one-fifth total length of body. Opercular about two-fifths of head length. Vertebrae about 30: abdominal 17, caudal 13. Pelvic 8, anal 12, dorsal 12. Origin of pelvic fin behind origin of dorsal.

REMARKS: Jordan (1910) considered *Dastilbe* (pl. 4, fig. 1) to be most nearly related to the clupeid *Halecopsis* from the Lower Eocene of Europe. There are obvious differences, however, such as the expanded preopercular and relatively smaller opercular in the latter. The resemblances between these genera would appear to be due more to the fact that they are both relatively primitive generalized Isospondyli than that they are actually near relatives.

Arambourg (1935b) transferred *Dastilbe* to the Chanidae, a family considered to be in

some respects more primitive than the Clupeidae and more closely related to the Albulidae. It includes the genus *Chanos*, which occurs in the Eocene and Miocene of Europe, and the Recent "milk fishes." Arambourg emphasizes the persistent notochordal canal and the stegurous type of terminalization (pl. 4, fig. 2) for the vertebral column as two important retained primitive characters. These, he believes, together with the observable skull characters and scale morphology, indicate that *Dastilbe* should be placed in the Chanidae.

This author has further pointed out that a series of leptolepids such as the Lower Jurassic *L. coryphaenoides*, Upper Jurassic *L. sprattiformes*, Upper Jurassic *L. brodiei*, and the Lower Cretaceous *L. formosus*, together with *Dastilbe* and the related Lower Cretaceous *Parachanos*, represent a structural series demonstrating the morphological transition, particularly in the structure of the caudal fin, from the paleoniscid stage to a stage represented by the clupeids. In such a series, it is possible to observe a reduction in the size of the notochordal canal, a change from the stegurous to homocercal type of caudal fin, and a gradual loss of ganoine on the scales.

While the presence of a persistent notochordal canal in the leptolepids and certain of the Chanidae may be considered as a truly primitive character, a hold-over from the holostean stage, it would appear that this character is of questionable phylogenetic value in more specialized groups in which it appears. Its occurrence in characins such as the Pliocene *Eobrycon* and the Recent *Brycon* and even in certain carangids suggests an independent retention of an embryonic condition. The presence of a notochordal canal in adult actinopterygians must be considered as a case of neoteny, and it may or may not be a primitive character, depending on the phylogenetic position of the group under consideration.

In adult actinopterygians, the stegurous condition of the caudal fin likewise represents the retention of an embryonic character that is very pronounced in the larval stages. Unlike the character discussed above, however, there is little reason for believing that neoteny has caused the retention of the stegurous caudal fin in any of the teleost groups beyond

the Clupeoidea and several of the derived suborders such as the Salmonoidea.

REFERRED SPECIMENS: A.M.N.H. Nos. 10018-10045.

FAMILY CLUPEIDAE

GENUS *KNIGHTIA* JORDAN, 1907

Diplomystus COPE, 1877, p. 811 (in part).

Knightia JORDAN, 1907, p. 136.

Ellipes JORDAN, 1910, p. 24 (Brazilian species only).

Ellimma JORDAN, 1913, p. 79 (new name for *Ellipes* Jordan, 1910, preoccupied).

Ellimma, JORDAN AND GILBERT, 1919, p. 26.

GENOTYPE: *Knightia eocaena* Jordan.

REVISED GENERIC DIAGNOSIS: Double-armed clupeids of varying body depth. Cleft of mouth moderately oblique. Teeth very small or absent. Vertebrae 31-36, caudals with double lateral laminae. Origin of pelvic behind origin of dorsal. Anal fin small, 12-14 rays. Dorsal scutes ovate with median carina and with or without extended posterior median spine. Ventral scutes of typical clupeoid type. Scales large, thin, smooth.

REMARKS: The inclusion of *Ellimma branneri* Jordan within the genus *Knightia* has necessitated a revision of the generic diagnosis of *Knightia*, particularly in regard to the nature of the dorsal scutes. As the latter genus is here understood, it includes the following species: *eocaena*, *alta*, *copei*, *branneri*, *brasiliensis*, and, tentatively, *elmodenae* and *barbarae*. The last two species, from the Miocene of California (Jordan and Gilbert, 1919), have not been available for study. The validity of *copei* (Tanner, 1925), described from a single specimen, is open to question as it may very well fit into the range of *alta*.

Knightia branneri (Jordan), 1910

Ellipes branneri JORDAN, 1910, p. 25, pl. 8, fig. 3.

Ellipes riacensis JORDAN, 1910, p. 28, pl. 10.

Ellimma branneri, JORDAN, 1913, p. 79.

TYPE: C. M. No. 5249/1. Complete specimen excepting imperfectly preserved fins.

HORIZON AND LOCALITY: Série Alagoas, ?Upper Eocene, Riacho Doce, Alagoas.

REVISED SPECIFIC DIAGNOSIS: Standard length ranging from 2.20 to 8.70 cm., depth from 1.05 to 4.00 cm. Head about one-quarter total body length. Opercular with striations radiating ventrally from point of

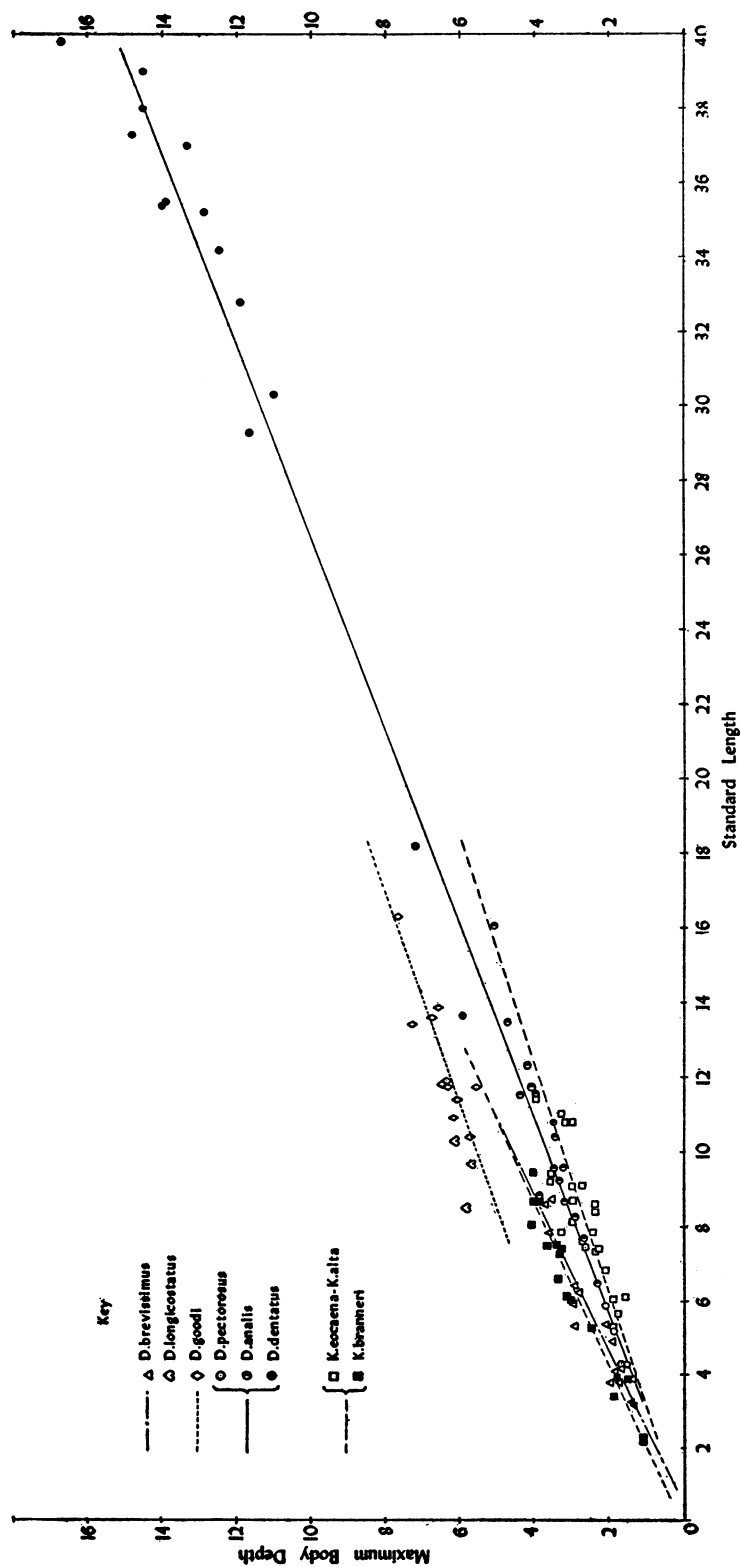
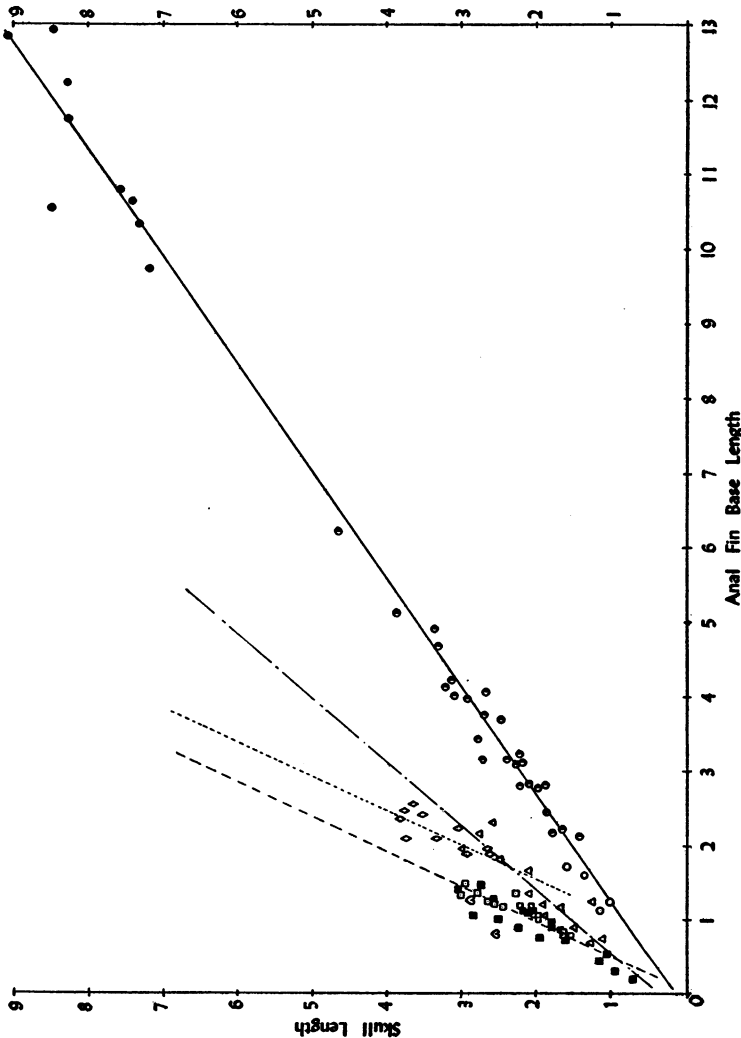


FIG. 3. Graph, in centimeters, of standard length (tip of premaxillary to end of last caudal centrum) and maximum body depth in eight species of double-armed herrings. In both *Diplomysus* and *Knightsia* there is a strong correlation between these two characters. The close grouping of the observations and the proximity and tendency towards parallelism of the trends for each species indicate the danger of employing such characters in separating these species. In spite of the distinctness of *D. dentatus* because of size, its trend coincides exactly with that of *D. analis* and *D. pectorosus*.

FIG. 4. Graph, in centimeters, of anal fin base length and skull length (anterior border of premaxillary to posterior border of opercular) in the same eight species of double-armed herrings. In this correlation there is a wide divergence of the *Knighia* and Green River diplomystids show a close grouping about a single trend, as do all the species of *Knighia*. The trend of *D. brevisimus* is intermediate in position, supporting the view that this species may belong to the central stock from which the other double-armed herrings were derived. The trend of *D. goodi* likewise occupies an intermediate position and almost parallels that of *Knighia*, a result of the short anal fin. The dorsal scutes, however, indicate affinity with *D. brevisimus*. The still shorter anal fin of *D. longicos-tatus* places the very few observations on this species close to the *Knighia* trend. The dorsal scutes again indicate a close relationship with *D. brevisimus*. Symbols same as in figure 3.



attachment. Vertebrae 31–33; abdominal 15–16, caudal 17. Dorsal fin 12, pectoral fin 8, anal fin 12. Origin of pelvic fin behind origin of dorsal fin and midway between origin of pectoral and origin of anal fins. Dorsal scutes widely ovate, lacking posterior spine.

REMARKS: This species (pl. 5, figs. 1, 2) was placed in a separate genus by Jordan because he considered its squamation to differ from that found in either *Diplomystus* or *Knightia*. He did state, however, that it possesses characters found in both these genera. The scales are well preserved in a number of specimens, and they appear to agree very closely in size and shape with those of *K. eocaena* and *alta*, being much larger than the scales of *Diplomystus*. The dorsal scutes (fig. 5) lack the lateral wings typical of *Diplomystus* and agree in their ovate configuration with those of *Knightia*, with the exception that the posterior border is not produced into a long spine.

The general body form is very similar to that found in *K. alta*, although the dorsal border, in mature individuals of *K. branneri*, tends to rise to a slight degree to an apex at the point of origin of the dorsal fin. A similar dorsal outline is characteristic of *Diplomystus longicostatus* and *D. goodi*, and affinity with these species might be considered were it not for the differences in the shape of the dorsal scutes and in the squamation.

Jordan (1910) recognized a second species of the genus *Ellipes* from Riacho Doce, which he named *E. riacensis*. He considered it to differ from *branneri* in having a relatively longer head, shorter mandible and ribs, more elongate body, and broader opercular. A restudy of Jordan's specimens does not reveal any consistent differences between the two species. The skull is not relatively larger in individuals of the same size, and the other proportions appear to be identical in specimens formerly assigned to each species. *E. riacensis* is therefore considered to be a synonym of *K. branneri*.

Woodward (1939) has described *Knightia brasiliensis* from Tertiary deposits at Nova York, Maranhão. It resembles *K. alta* with a flattened dorsal border and rather deep body. The dorsal scutes are not described excepting that they lack lateral wings.

REFERRED SPECIMENS: A.M.N.H. Nos. 10046–10062.

GENUS *DIPLOMYSTUS* COPE, 1877

Diplomystus COPE, 1877, p. 811.

GENOTYPE: *Diplomystus dentatus* Cope, 1877. (For generic diagnosis, see Thorpe, 1938, p. 280.)

Diplomystus longicostatus Cope, 1885

Diplomystus longicostatus COPE, 1885, p. 3.

Diplomystus longicostatus, WOODWARD, 1888, p. 134.

Diplomystus longicostatus, WOODWARD, 1895, p. 2, pl. 1.

Diplomystus longicostatus, WOODWARD, 1901, p. 143.

Ellipes longicostatus, JORDAN, 1910, p. 29, pl. 11.

Ellimmichthys longicostatus, JORDAN, 1919, p. 27.

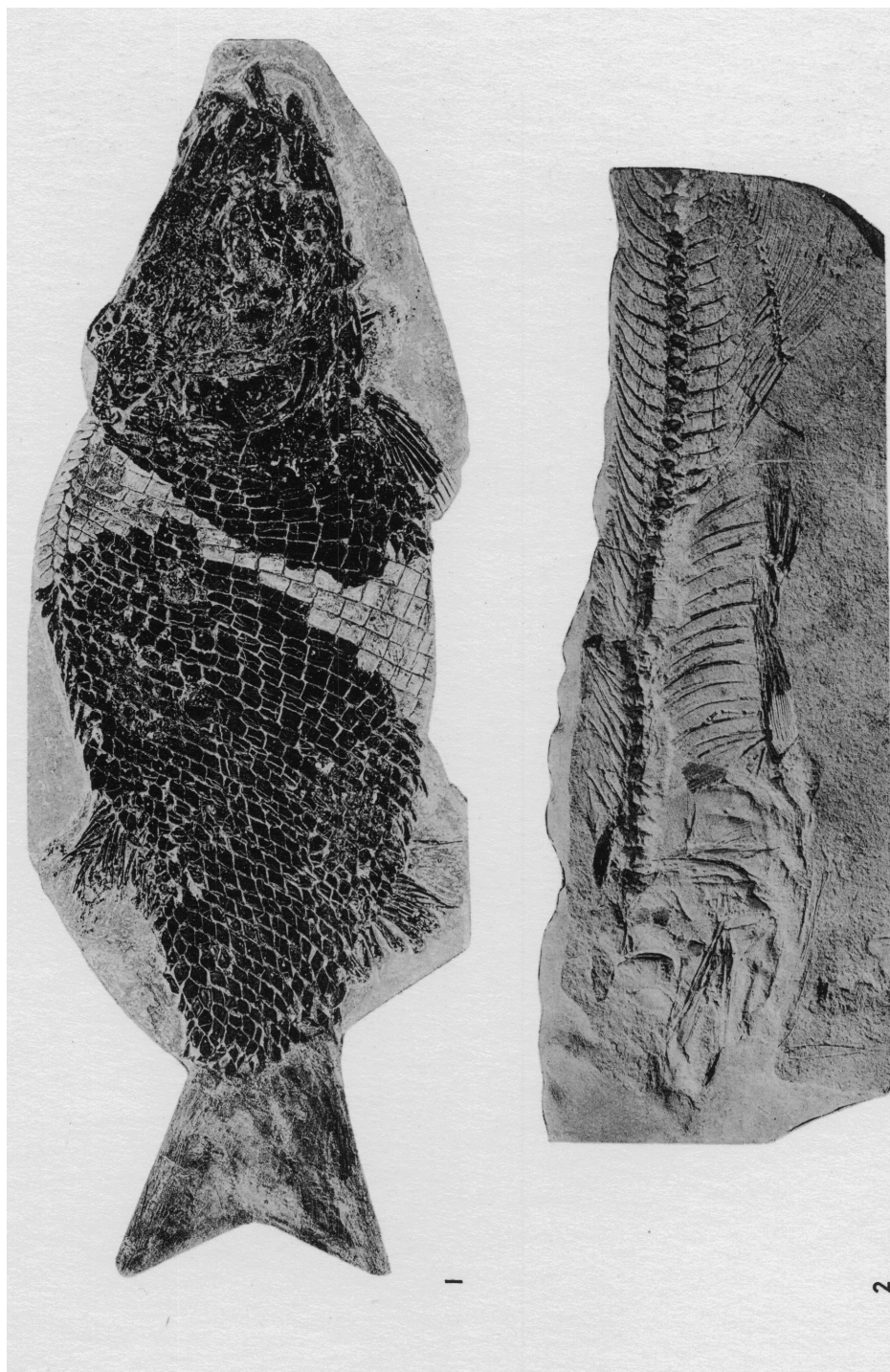
TYPE: Status unknown; should be in American Museum of Natural History but cannot be located.

HORIZON AND LOCALITY: Série Baía, Upper Cretaceous, between Plataforma and Itacarânia, along eastern shore of Baía de Todos os Santos, Baía.

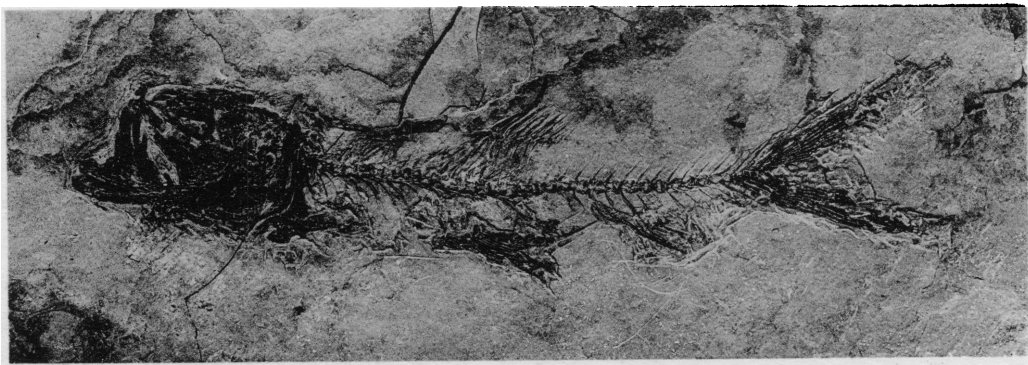
REVISED DIAGNOSIS: Standard length 8.50 to 10.30 cm., greatest depth from 5.80 to 6.15 cm. Head about one-third total body length. Dorsal outline rising sharply to apex at origin of dorsal fin with equally sharp descent posteriorly. Body very deep with ventral border markedly concave. Vertebrae about 36: abdominal 24, caudal 10–12. Dorsal fin 10, pectoral fin 9, pelvic fin 6–7, anal fin 8. Origin of pelvic fin opposite origin of dorsal, origin of anal midway between origin of dorsal and origin of caudal fins. Pelvic fin smaller than pectoral. Dorsal scutes with lateral wings, posterior border not denticulated. Ventral scutes enlarged behind pelvic fin.

REMARKS: Although *D. longicostatus* (fig. 5) is not included in the collection under consideration, it is represented by two specimens on a single slab of unknown origin from the Newberry Collection, A.M.N.H. No. 734. A reconsideration of its systematic position is desirable as Cope (1895) considered it to be allied to *Knightia* (*D. humilis*), presumably because the dorsal scutes are cordate. The dorsal scutes of one specimen show lateral

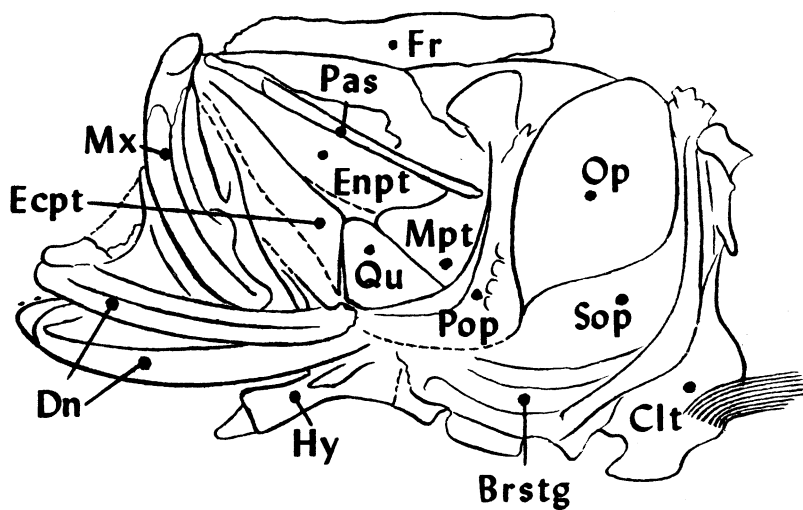
PLATES 1-7



1. *Lepidodus piauhyensis* Roxo and Löfgren. A.M.N.H. No. 10012. Outline of caudal fin and portion of body restored. Two rounded excrescences are present on the flank of this specimen. $\times 3/7$
 2. *Lastroichthys longipectoralis*, new genus and species. A.M.N.H. No. 10017. Type specimen. $\times 2/5$



1

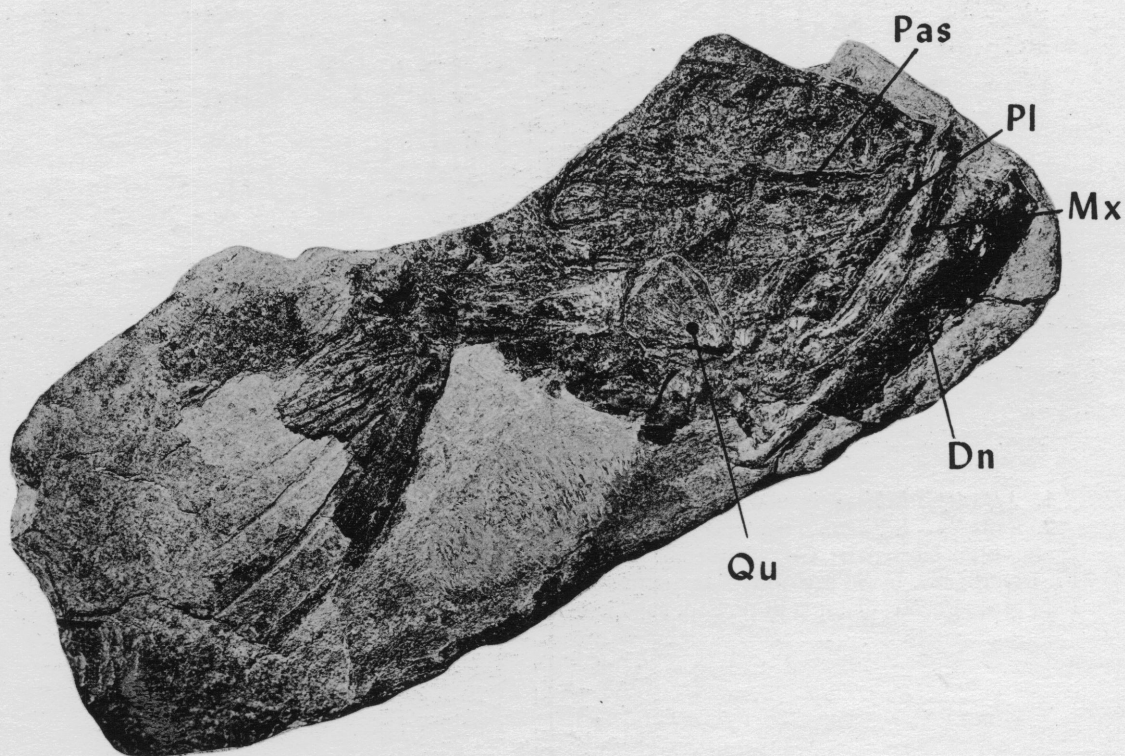


2

1. *Leptolepis bahiaensis*, new species. A.M.N.H. No. 10014. Type specimen. $\times 2/1$
2. *Leptolepis bahiaensis*, new species. Outline drawing of skull as preserved in type. *Abbreviations:* Brstg, branchiostegals; Clt, cleithrum; Dn, dentary; Ecpt, ectopterygoid; Enpt, entopterygoid; Fr, frontal; Hy, hyoid arch; Mpt, metapterygoid; Mx, maxillary; Op, opercular; Pas, parasphenoid; Pop, preopercular; Qu, quadrate; Sop, subopercular. $\times 6$

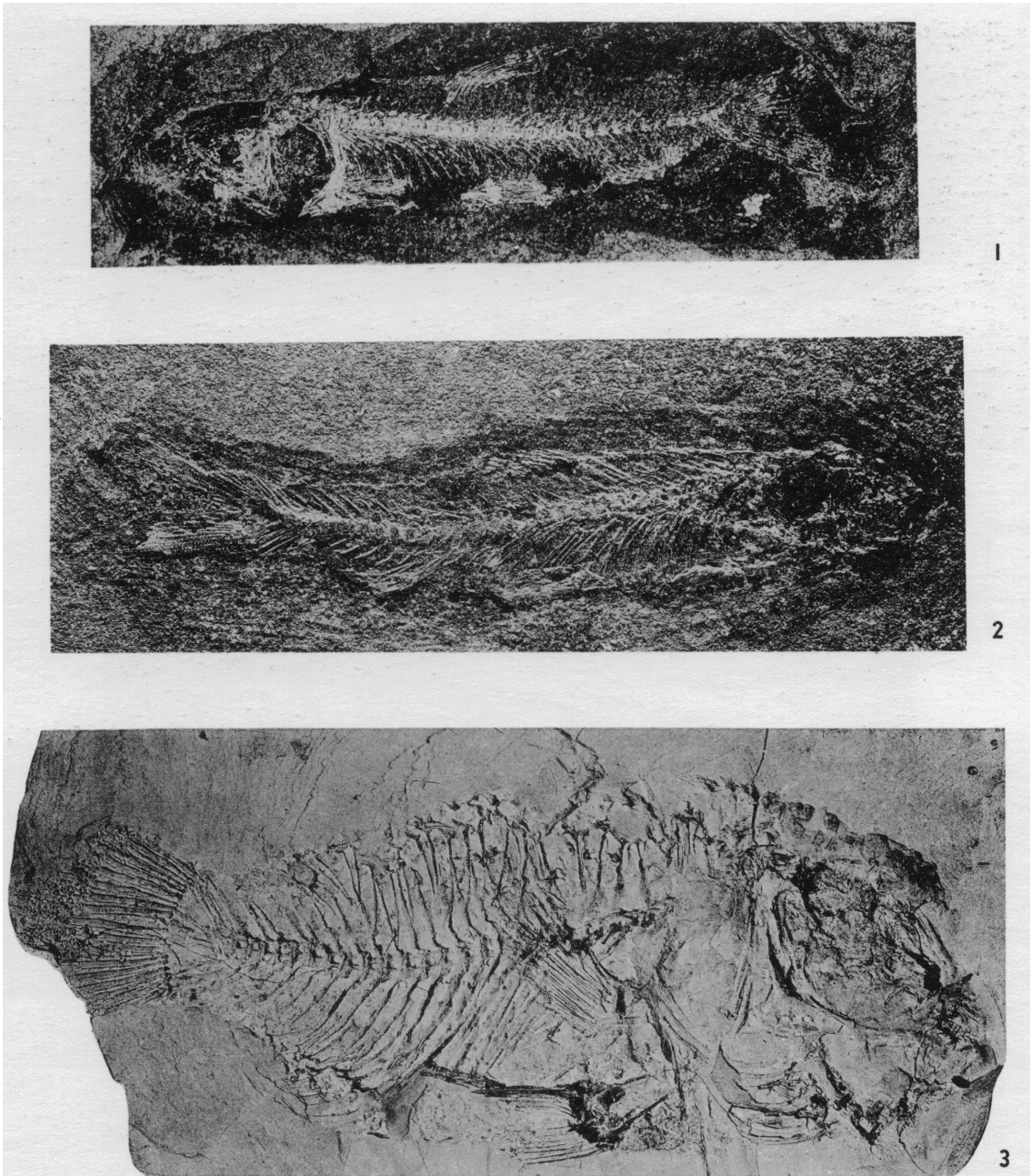


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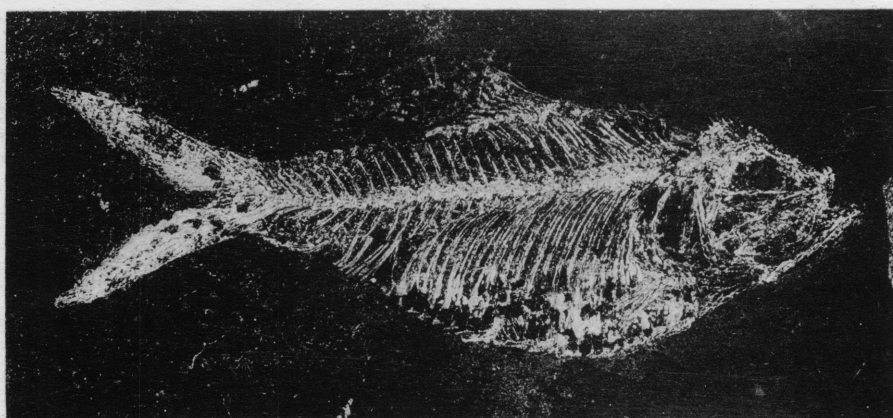
1. *Chiromystus alagoensis* Jordan, A.M.N.H. No. 10015. $\times 2/3$
2. *Chiromystus alagoensis* Jordan, type. C.M. No. 5246/100. Skull and pectoral fin. Abbreviations: Dn, dentary; Mx, maxillary; Pas, parasphenoid; Pl, palatine; Qu, quadrate. $\times 1/1$



1. *Dastilbe crandalli* Jordan. A.M.N.H. No. 10034. Positions of the fins well indicated. The skull is poorly preserved in all available specimens. $\times 3/2$
2. *Dastilbe crandalli* Jordan. A.M.N.H. No. 10028. The stegurous terminalization of the vertebral column is clearly demonstrated in this specimen. $\times 4/3$
3. *Aequidens pauloensis*, new species. A.M.N.H. No. 10095. Type specimen. The dorsal fin is missing and the anal fin not completely preserved. $\times 3/4$



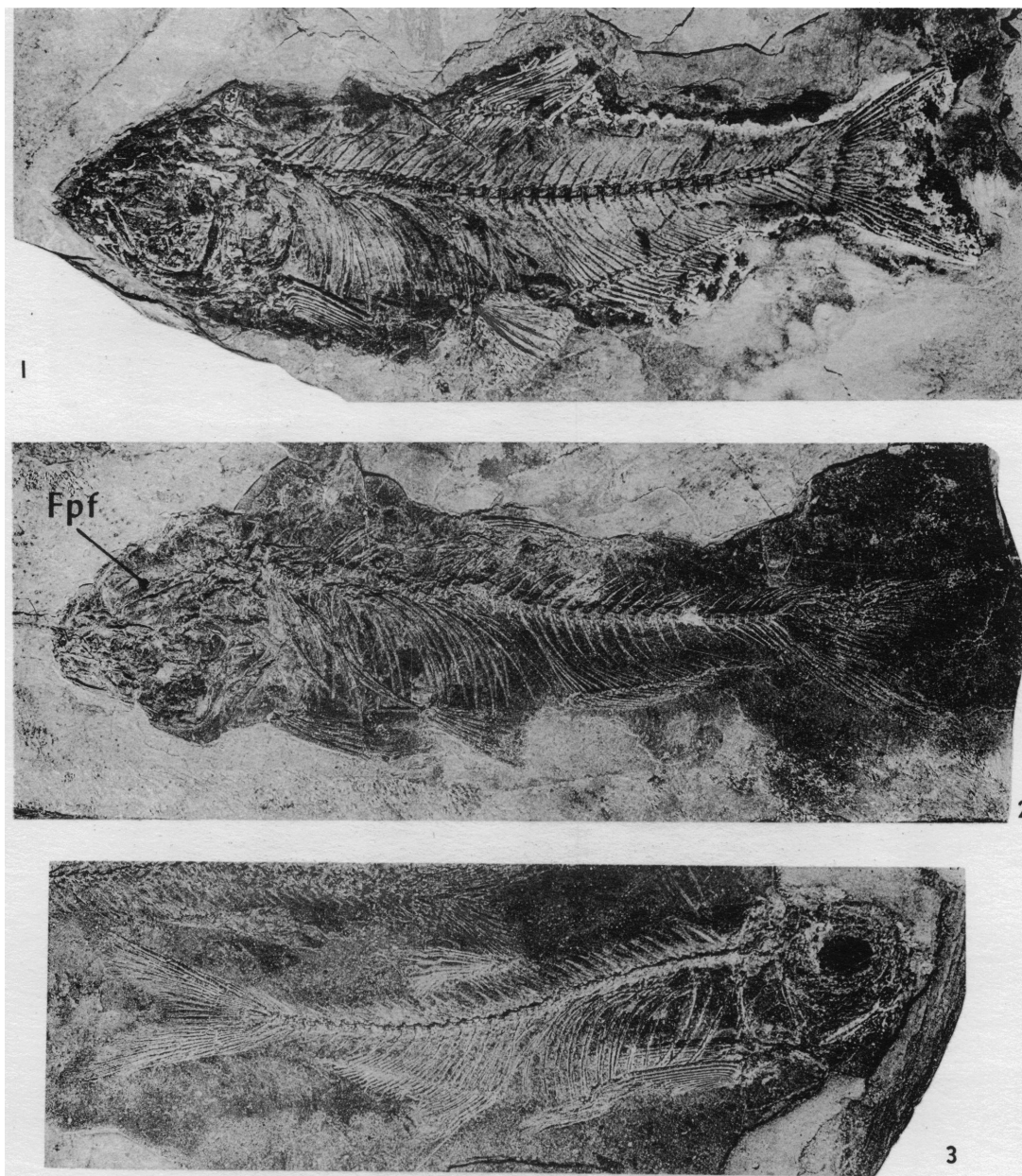
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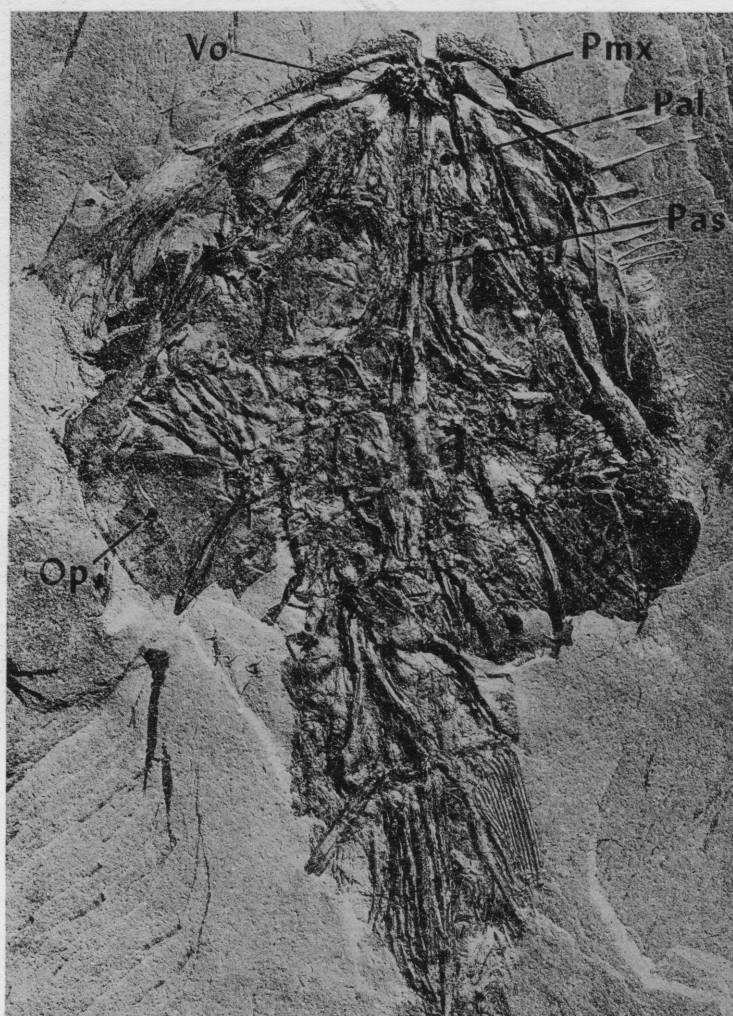
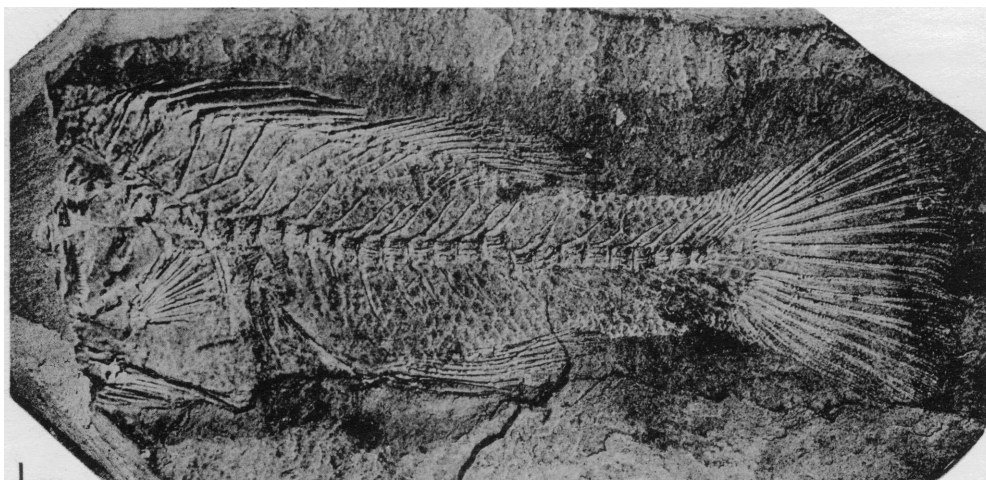
2

1. *Knightia branneri* (Jordan). C.M. No. 5248/4. This specimen is the type of *Ellipes riacensis* Jordan. $\times 4/5$

2. *Knightia branneri* (Jordan). A.M.N.H. No. 10057. There is no indication in this specimen of the elevation of the dorsal border present in figure 1. This character is highly variable within the species and may be partly a result of poor preservation. $\times 1/1$



1. *Eobrycon avus* (Woodward). A.M.N.H. No. 10070. Pelvic fin restored. $\times 4/5$
2. *Eobrycon branneri* Eigenmann. A.M.N.H. No. 10089. Type specimen. Fpf, fronto-parietal fontanelle. $\times 4/5$
3. *Eobrycon ligniticus* (Woodward). A.M.N.H. No. 10067. $\times 3/2$



1. *Percichthys antiquus* Woodward. A.M.N.H. No. 10091. Portion of the preopercular is preserved showing the serrated posterior border. $\times 1/2$

2. *Percichthys antiquus* Woodward. A.M.N.H. No. 10092. Impression of the ventral surface of the skull. Abbreviations: Op, opercular; Pal, palatine; Pas, parasphenoid; Pmx, premaxillary; Vo, vomer. $\times 3$

wings, a fact pointed out by Woodward (1901), indicating that this species, now considered to be Upper Cretaceous rather than Lower, should be included in *Diplomystus*. Jordan (1910) included *D. longicostatus* in *Ellipes* but failed to state the reason and later (1919) placed it in a separate genus, *Ellimmichthys*, principally because of the high elevation of the dorsal border. As the latter is a character apparently occurring in both *Knightia* and *Diplomystus*, it cannot be considered of generic value.

The resemblance between *D. longicostatus* and *D. goodi* (Eastman, 1912; Weiler, 1923a, 1923b) from the Tertiary of West Africa is very close, and they can be distinguished mainly by a probable significant difference in the shape of the dorsal scutes (difficult to determine in the case of *D. goodi*) and a different vertebral count.

PRELIMINARY ANALYSIS OF THE DOUBLE-ARMORED CLUPEIDS

Cope long ago recognized the need for separating *Diplomystus* into two sections, mainly because of a difference in the shape of the dorsal scutes. Jordan (1907), in agreement, elevated one of these sections to the rank of the separate genus *Knightia*. In order to determine further the validity of assigning the species formerly grouped under *Ellimma* to *Knightia*, *Ellimmichthys longicostatus* back again to *Diplomystus*, and also to investigate the relationships between the various species of the two genera here recognized, four characters in nine species have been studied quantitatively.

As in the case of the scatter diagrams for *Eobrycon* to be discussed later, the regression for each species of *Diplomystus* and *Knightia* represents essentially an ontogenetic series rather than the range of variation within a population sample of adult individuals. An overlap between separate regressions does indicate similarity in body form, although the trends in some cases may be in somewhat different directions. This analysis is more or less tentative and is based only on the material available in the American Museum and some from the Carnegie Museum. The use of much larger samples and additional characters is contemplated in connection with a

study of the fish fauna of the Green River shales.

In figure 3 the standard length is plotted on the horizontal axis against maximum body depth on the vertical axis. In figure 4 the horizontal axis represents the length of the base of the anal fin and the vertical the length of the skull from the anterior border of the premaxillary to the caudal border of the operculum along a line represented by the parasphenoid. The species considered are *Diplomystus dentatus*, *analis*, and *pectorosus* from the Green River Middle Eocene, *D. longicostatus* from the Upper Cretaceous of Brazil, *D. brevissimus* from the Upper Cretaceous of Syria, *D. goodi* from the early Tertiary of West Africa, *Knightia eocaena* and *alta* from the Green River, and *K. branneri* from the possible early Tertiary of Brazil.

It would appear from inspection of the regressions that *D. dentatus* is quite distinct from the other species considered. The rather large collection of diplomystids from the Green River shales contains no individuals that are intermediate in size between *D. dentatus* and *D. analis*, a fact which is rather difficult to explain. The positively identified specimens of *D. dentatus* are all characteristically large, with apparently no younger stages represented. Although there very well may be some young of this species included in the *D. analis* scatter, these cannot be separated with any degree of certainty, particularly since the vertebral counts of the two species overlap. There is some evidence, however, of differences in the details of the dorsal scutes, and it may be possible to separate further specimens of the same size by counting the annular rings of the scales.

The separation between the regressions of *D. dentatus* and *analis* may be narrowed by the study of a larger series, although a survey of the literature indicates that this is not likely. Several possible explanations might be offered, for instance, a restriction of the young of *D. dentatus* to a particular type of environment such as the running water of streams or shallow water near the edge of the Green River lakes. Individuals segregated under such conditions either might not have been preserved or have not thus far been collected.

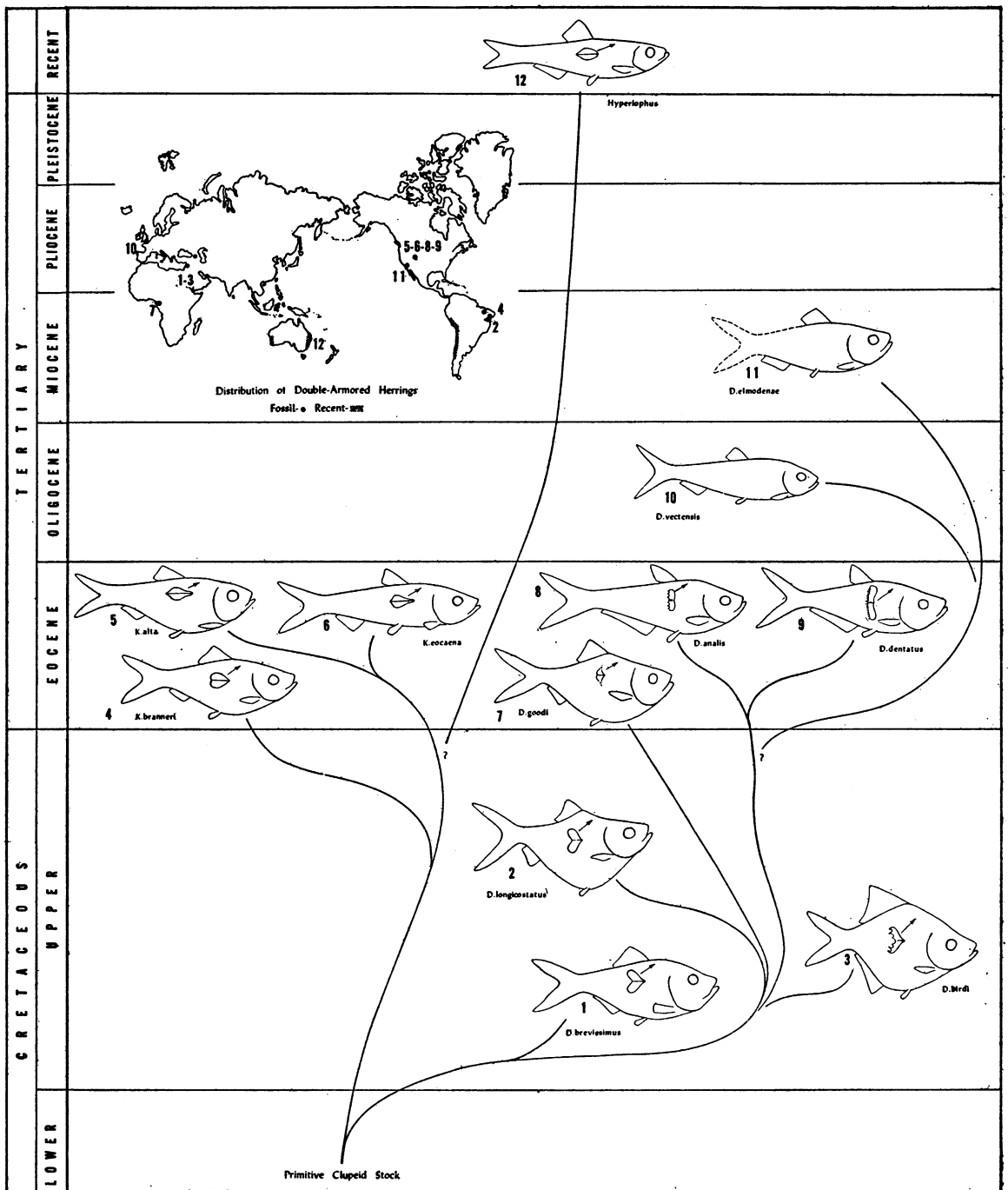


FIG. 5. Tentative phylogeny of the double-armed herrings. Not all of the species represented in the distribution map are included in the phylogeny. The dorsal scutes, where known, are outlined. On the basis of the graphs (figs. 3 and 4) and the shape of the dorsal scutes, it is possible to recognize three phylogenetic trends. The first includes *D. brevissimus*, *D. longicostatus*, and possibly *D. goodii*; the second includes the *Knighthia* group; and the third includes the Green River diplomystids. *D. birdi* may possibly be ancestral to the Green River forms through the *D. brevissimus* stock. The dorsal scutes of *D. vectensis* and *D. elmodenae* have not been described, and the position of these species is questionable.

The regressions of the other species of both *Diplomystus* and *Knightia* are clustered together for both sets of characters studied. In figure 3 the regressions for *Knightia alta* and *eocaena* run imperceptibly into one another, bearing out Thorpe's statement (1938) that in a large series it is very difficult to separate these species. Their status will be further considered in the Green River fauna study. The more deep-bodied individuals, identified as *alta*, overlap the regressions of *Diplomystus analis*, *pectorosus*, and *brevissimus*. This situation is not surprising since the body form in the two genera is almost identical, particularly in species with short anal fins. In the Green River diplomystids only, the anal fin is relatively long and the ventral border in the caudal region is hence quite straight, resulting in a rather distinctive body outline. *D. longicostatus* and *D. goodi* represent the extreme in body depth as their regressions demonstrate.

In figure 4, in which the length of the base of the anal fin is plotted against skull length, the relatively long anal fin and shorter skull distinctly separate the Green River diplomystids from the other species of this genus and also from *Knightia*. The regressions for *Knightia branneri* and *K. eocaena* plus *alta* are completely superimposed, further supporting the assignment of *branneri* to this genus. The shorter anal fin and longer skull combination has also developed within the diplomystids, accounting for the proximity of *D. longicostatus* and *D. goodi* with *Knightia*.

A feature of the body form that is difficult to present quantitatively is the elevation of the dorsal border, a character that has apparently developed in both genera. This elevation is associated with the relative increase in skull length and decrease in anal fin length.

Diplomystus birdi from the Upper Cretaceous of Syria, with its hypsomatic body form, may represent a side-line developed from the early diplomystid stock. Its extreme depth is analogous to that found in such a form as *Zanclus*, and as is characteristic of such types, the dorsal and anal fins are opposite one another. The dorsal scutes are strongly denticulated and rather resemble those of *D. dentatus*. *D. brevissimus* from the same locality, on the other hand, is far more generalized with dorsal scutes that have a smooth posterior border.

A tentative phylogeny of the double-armored clupeids (fig. 5), based on the present study, indicates the changes in body form that have occurred since the Lower Cretaceous. The first true generalized clupeids occur in the Lower Cretaceous, and it would appear that the rough-backed herrings were differentiated from the primitive clupeoid stock at about that time. The extreme depth of the body in *D. longicostatus* further suggests that a tendency in the deep-bodied direction appeared about as early as the transformation of the middorsal scales into scutes. (Woodward, 1942, p. 908, considers the dorsal and ventral ridge scutes to be a direct "ganoid" inheritance.) The Cretaceous diplomystids are all fairly deep bodied as are all but one species of *Knightia*. The tendency towards a fusiform body outline seems to represent more of an end development, appearing in the Eocene *K. eocaena*, the Oligocene *D. vectensis*, and the Recent *Hyperlophus*, *Potamolosa*, and *Ethmidium*.

Diplomystus brevissimus could very well represent the generalized type from which *Knightia*, the other species of *Diplomystus*, and the Recent double-armored herrings are derived. The body is moderately deep, the dorsal scutes have poorly developed lateral wings, and the anal fin is of moderate length. It is likely, however, that the two types of dorsal scutes developed in the Lower Cretaceous, although *Knightia* is unknown before the Lower Tertiary or Upper Cretaceous of Brazil (Série Alagoas). The difference in scale size, mentioned above, also must have developed at this time.

The dorsal scutes of the Oligocene and Miocene diplomystids have not been adequately described. Woodward (1901) states that those of *D. vectensis*, from the Oligocene of the Isle of Wight, are "narrow," while the dorsal scutes of *K. elmodenae* (Jordan, 1919) are "simple." It is very possible that *D. vectensis* should be transferred to *Knightia*. Smirnov (1935, 1936) has described *Diplomystus brevicaudus* and *D. alter* from the north Caucasus, but unfortunately the published descriptions have not been available for comparison with the other members of this genus. It is becoming evident, however, that the double-armored herrings had a world-wide distribution probably from the Cretaceous through the greater part of the Tertiary.

During this long period they inhabited fresh, brackish, and salt water and consequently cannot be considered as being typically associated with any of these habitats.

Three Recent genera are assigned to this group. *Hyperlophus* is known from the coastal waters of Australia and is probably most nearly related to *Knightia*. The dorsal scutes of several specimens of *Hyperlophus spratellides* in the American Museum collection are ovate with a spinous carina projecting somewhat beyond the posterior border. The scutes resemble those of *K. eocaena* in general outline, and the shallow, fusiform body is very similar to that found in this species. The scales are likewise large and thin.

Potamalosa, presumably closely related to *Hyperlophus*, occurs in fresh water and is apparently restricted to the coastal rivers of New South Wales. *Ethmidium* inhabits the coastal waters of Peru and Chile and is very similar in body form to the genera from Australia. These Recent forms can be considered only as isolated remnants of a group that was undoubtedly universally distributed until the later Tertiary.

In many respects it appears desirable to establish a separate family for the double-armored herrings. The presence of the dorsal scutes certainly sets this group apart from the other clupeids, which otherwise may be divided into two sections according to the presence or absence of the ventral scutes. The taxonomy of the *Diplomystus-Knightia* complex is, however, still unsatisfactory. In many cases, the specific differences disappear when large series of specimens are available, for instance between *K. eocaena* and *K. alia*. Even the distinction between these two genera is not sharply defined because of intergrading forms such as *K. branneri*. It is hoped that the large series of specimens of all species to be employed in the study of the Green River fauna will aid in resolving, through a further quantitative analysis, this rather confusing picture.

The presence of a denticulated posterior border on the dorsal scutes of the Green River diplomystids has been generally considered as a generic character of some importance (Thorpe, 1938). It is evident, however, that by no means all of the species assigned to *Diplomystus* possess this character. Both

D. longicostatus and *D. brevissimus*, for instance, have dorsal scutes with a smooth posterior border and wide, rounded, lateral wings. Although the term cordate has been employed to describe the dorsal scutes of *Knightia*, it more nearly fits the shape of these plates in most species of *Diplomystus*. Those of the Green River species and of *D. birdi* with narrow lateral wings and a denticulated posterior margin can be considered only as modifications of a basic cordate type. A possibly more appropriate term for the shape of the dorsal scutes in *Knightia* is ovate, as they lack the posterior notch which in effect produces the lateral wings. As is evident, such finely drawn distinctions become almost meaningless when the less specialized diplomystids are compared with *Knightia*, and there is no doubt that the differences between *Diplomystus* and *Knightia* are of much less significance than they were considered to be by Jordan. A comparison of these genera from the Green River shales only by no means presents the true picture.

ORDER OSTARIOPHYSI

SUBORDER CYPRINOIDEA

FAMILY CHARACINIDAE

GENUS *EOBRYCON* JORDAN, 1907

Tetragonopterus Cuvier, 1817, (in part) WOODWARD, 1898, p. 66.

Eobrycon JORDAN, 1907, p. 140.

GENOTYPE: *Tetragonopterus avus* Woodward.

REVISED GENERIC DIAGNOSIS: Fusiform, moderately deep-bodied fishes with rounded ventral border as in recent *Brycon*. Length of anal fin base about three-fourths of skull length. Fronto-parietal fontanelle present. Premaxillary teeth with three cusps arranged in linear order as in *Brycon*. Vertebral centrum with single lateral ridge. Notochordal canal relatively larger than in *Brycon*. Ribs robust, not quite reaching ventral border, with single longitudinal groove. Anal fin extended. Fork of caudal fin shallow. Dorsal fin short based. Pectoral rays extend beyond origin of pelvic.

Eobrycon avus (Woodward), 1898

Tetragonopterus avus WOODWARD, 1898, p. 66, fig. 3.

Tetragonopterus avus, WOODWARD, 1901, p. 298, pl. 17, fig. 1.

Eobrycon avus, JORDAN, 1907, p. 140, fig. 31.

Eobrycon avus, EIGENMANN AND MYERS, 1929, p. 513.

TYPE: B.M.N.H. No. P. 9222. Complete fish with imperfectly preserved skull.

HORIZON AND LOCALITY: ?Pliocene beds exposed at Taubaté and Tremembé, São Paulo.

REVISED SPECIFIC DIAGNOSIS: Standard length ranging from 8.60 to 17.60 cm., greatest depth from 1.85 to 4.05 cm. Skull about one-fourth total body length. Vertebrae 38–42: abdominal about 20, caudal about 22. Dorsal fin 10–11, pectoral fin 9–11, pelvic fin 8–9, anal fin 22–23. Origin of dorsal fin midway between origin of pectoral and origin of anal fins.

REFERRED SPECIMENS: A.M.N.H. Nos. 10063–10066, 10070–10088.

Eobrycon branneri Eigenmann, 1929

Eobrycon branneri EIGENMANN, 1929, p. 514, pl. 81.

TYPE: A.M.N.H. No. 10089. Complete fish with well-preserved fins. Type and paratype (A.M.N.H. No. 10090) donated to the American Museum of Natural History by Indiana University.

HORIZON AND LOCALITY: ?Pliocene beds exposed at Taubaté, São Paulo.

REVISED SPECIFIC DIAGNOSIS: Length of skull plus vertebral column in type and paratype (only known specimens) 13.2 and ± 14.7 cm., greatest depth 4.00 and 5.15 cm. Skull more than one-fourth total length of body. Vertebrae about 38: abdominal about 20, caudal 18. Ray counts about as in *E. avus*. Origin of dorsal midway between origin of pelvic and origin of anal.

Eobrycon ligniticus (Woodward), 1898

Tetragonopterus ligniticus WOODWARD, 1898, p. 67, figs. 4, 5.

Tetragonopterus ligniticus, WOODWARD, 1901, p. 298, pl. 17, figs. 2, 3.

Lignobrycon ligniticus, EIGENMANN AND MYERS, 1929, p. 513.

TYPE: B.M.N.H. No. P. 9012. Complete fish.

HORIZON AND LOCALITY: ?Pliocene beds

exposed at Taubaté and Tremembé, São Paulo. Lacustrine-fluvial.

REVISED SPECIFIC DIAGNOSIS: Length of skull plus vertebral column ranging from 4.45 to 8.60 cm., maximum depth from 1.07 to 2.20 cm. Body similar to *E. avus* and *E. branneri*. Opercular not striated. Orbit relatively large, about one-third of skull length. Teeth as in preceding species. Vertebrae 38: abdominal 18, caudal 20. Dorsal 8, pectoral 11, pelvic about 7, anal about 30. Origin of dorsal above origin of anal.

REFERRED SPECIMENS: A.M.N.H. Nos. 10067–10069.

REMARKS: The taxonomic history of *E. ligniticus* represents an interesting comparison between the approach of paleoichthyologists and neoichthyologists to the problem of the relative value or importance of single characters in a fossil teleost. Woodward, representing the former group, placed *E. avus* and *E. ligniticus* in the same genus, considering the differences to be of specific value only. Eigenmann and Myers, representing the latter, considered *E. ligniticus* to be worthy of separate generic rank on the basis of the position of the dorsal fin, but admitted that in other respects it resembles *Eobrycon*. Discussion with a neoichthyologist confirms the attitude of the latter authorities, namely, that the position of the dorsal may be a character of generic significance in Recent fishes and that a difference in position, separating two genera, is usually accompanied by other diagnostic differentiation, for instance in squamation, which is usually observable only in the living fish. Hence the two groups of students, using a somewhat different approach, are prone to place different values on the available differentiating characters in the fossil forms. Where accurate, conclusive, quantitative work is not possible because of the nature of the material, a more conservative approach would appear desirable, even though such "lumping" of species may still be quite subjective.

In the genus *Eobrycon*,¹ as here recognized, the three species *avus*, *branneri*, and *ligniticus*

¹Santos has recently described *Lignobrycon altus* (1946, Notas Prelim. Estudos, Div. Geol. Min., Rio de Janeiro, no. 36, pp. 1–3, pls. 1–2) from the Lower Tertiary locality at Nova York, Maranhão. He considers it to differ from *L. ligniticus* in having a greater body depth and a smaller number of rays in the anal fin (26).

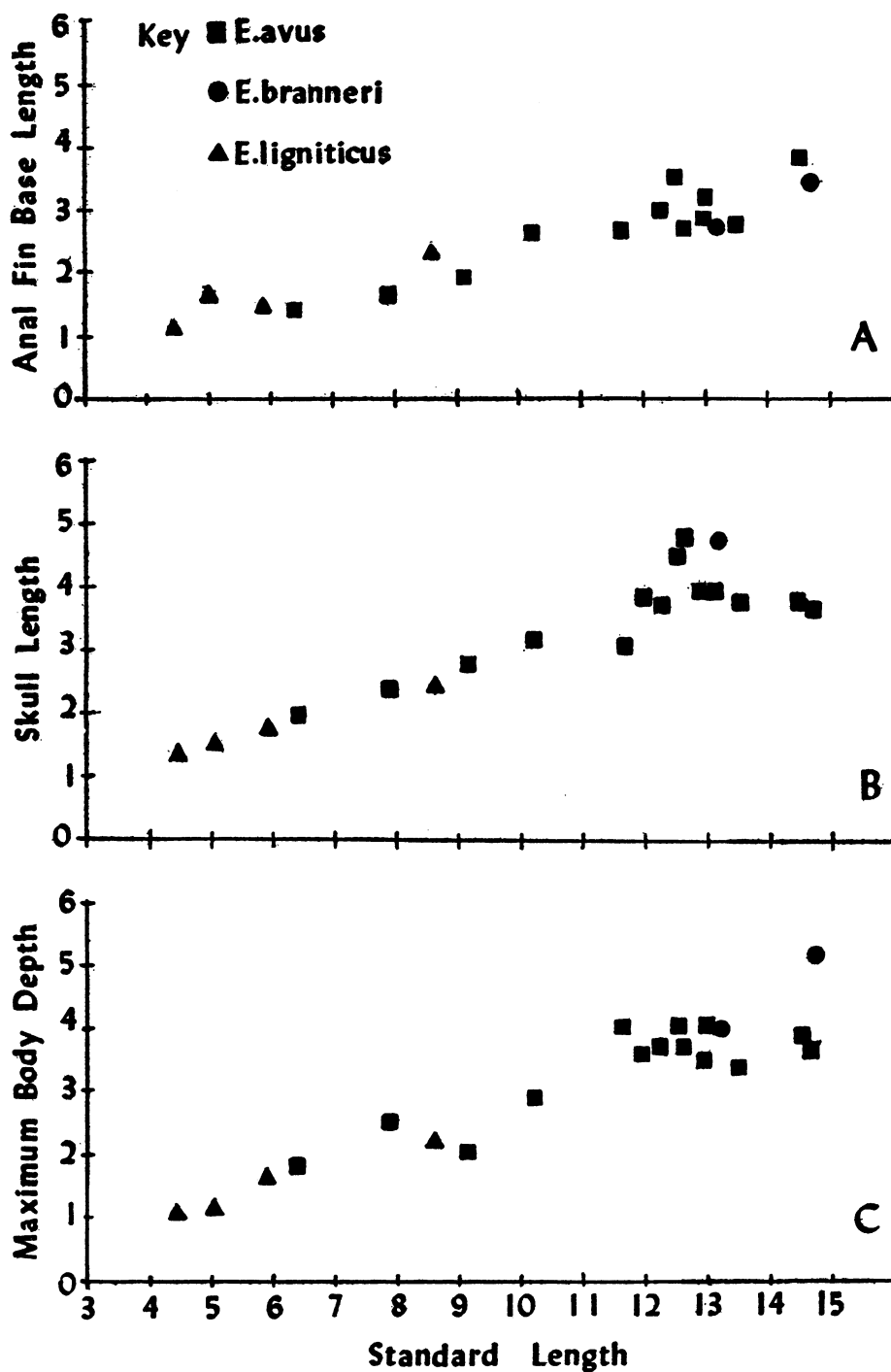


FIG. 6. A. Graph of anal fin base length and standard length in centimeters for the three species of *Eobrycon*. B. Graph of skull length and standard length in centimeters. C. Graph of maximum body depth and standard length in centimeters.

(pl. 6), in the order named, represent a series demonstrating three different positions of the dorsal fin from one essentially above the pelvic fin to one above the anterior portion of the anal fin. The location of the dorsal fin in *ligniticus*, therefore, would appear to lose its possible generic value. The orbit in *E. ligniticus* is apparently not relatively larger than in *E. avus*. An analysis of skull length compared with orbit length indicates that the orbit increases in size at a greater constant rate than the skull through *E. ligniticus* and *E. avus*.

A graphic comparison of the variation in total skull length, length of the base of the caudal fin and maximum body depth (vertical axis) with the standard length (horizontal axis) is made in figure 6. As previously pointed out, the distribution within each species represents essentially an ontogenetic series, and it cannot be considered as indicating the range of variation in a population of adult individuals. It is evident, however, that for the characters studied *E. ligniticus* grades into or overlaps *E. avus*, while *E. branneri* overlaps *E. avus* at the other end of its range. This analysis is simply another indication of the close affinity of the three species of *Eobrycon*. *Eobrycon branneri* may be distinguished from *E. avus* by the position of the dorsal fin and possibly a greater maximum body length. The small number of known specimens of the former species makes it impossible to determine with any degree of accuracy the amount of intraspecific variation and the degree of overlap with *E. avus*. *E. ligniticus* may be distinguished from the other two by its smaller body size, lack of radiating striations on the opercular bone, and, of course, the position of the dorsal fin.

The resemblance between *Eobrycon* and *Brycon* is very marked and appears to indicate a close affinity, if not synonymy, as noted by Eigenmann and Myers (1929, p. 514). Besides close resemblance in tooth form, nature of the fronto-parietal fontanelle and body shape, there is a very similar cheek-bone pattern in the two genera. They appear to differ in that *Eobrycon* has a narrowing of the operculum dorsally, a wider horizontal arm on the preopercular, and finally no indication of the anterior and posterior plate-like expansions of the interneurals, particularly in those anterior to the dorsal fin. It has not

been possible to confirm an indication of the adipose fin in the type of *Eobrycon branneri* as reported by Eigenmann and Myers.

Eobrycon, being so nearly related to a well-defined Recent genus, offers no information as to the origin of ancestry of the Characinae. The two characins described by Piton (1938) from the Middle Eocene lacustrine-fluvial beds at Menat, France, *Prohydrocyon pellegrini* and *Procharacinus arverniensis*, throw no light on the problem. The former has a small mouth, bordered above mostly by the premaxillary. The teeth are styliform and are arranged in two rows on the upper jaw and in a single row on the lower jaw. The general pattern and relative size of the cheekbones do not indicate a close relationship with the recent *Hydrocyon*. *Procharacinus* likewise has a small mouth, bordered above entirely by the premaxillary. The arrangement of the cheek bones appears very similar to that found in *Prohydrocyon*, but the number of teeth is much smaller than in this genus.

In our present state of knowledge regarding the phylogeny of the characins, it is difficult to determine the relationships of these genera. That they are not close to *Eobrycon* is quite certain.

Cockerell (1919) and David (1946) have described a characin, *Erythrinolepis*, from the marine Upper Cretaceous of California and Wyoming, and Cockerell (1921) has described another form, *Characilepis*, from beds at Huacho, Peru, which are probably marine Cretaceous. Both genera are based on isolated scales only. *Erythrinolepis* is probably related to the subfamily Erythrininae, an American group including the Recent *Erythrinus* and *Lebiasina*, but this relationship is not absolutely certain. *Characilepis* may be included in the subfamily Cheirodontinae of Gregory and Conrad (1938) or Tetragonopterinae of Eigenmann (1929) as the scale pattern bears a very close resemblance to that of the Recent *Bryconamericus*. The nature of the relationship is, however, again uncertain.

Although the fossil characin evidence is anything but illuminating, there is good reason for believing that the Characinae were undergoing a radiation by Upper Cretaceous time and that the subfamilies were established by the early Tertiary. If the scale

identifications can be considered as reliable, there is further evidence that this characteristically fresh-water family had marine members and possibly a marine origin in Cretaceous time, a problem that will be outlined further in the discussion.

ORDER ACANTHOPTERYGII

SUBORDER PERCOIDEA

FAMILY SERRANIDAE

GENUS *PERCICHTHYS* GIRARD, 1854

Percichthys GIRARD, 1854, p. 197.

GENOTYPE: *Perca trucha* Cuvier and Valenciennes. (For generic diagnosis, see Boulenger, 1895, p. 118.)

Percichthys antiquus Woodward, 1898

Percichthys antiquus WOODWARD, 1898, p. 68, figs. 6, 7.

Percichthys antiquus, WOODWARD, 1901, p. 514.

TYPE: Senckenberg Museum, Frankfurt, Germany. Number and status unknown. Imperfect fish lacking portion of dorsal and caudal. Figured by Woodward, 1898 (fig. 6).

HORIZON AND LOCALITY: ?Pliocene beds at Taubaté and Tremembé, São Paulo.

REVISED DIAGNOSIS: Probable length ranging from 11.20 to 20 cm. Greatest depth no less than 2.5 cm. Skull somewhat more than one-third total length of body. Posterior border of preopercular finely serrated. Vertebrae 32–35: abdominal 14–15, caudal 18–20. Anterior dorsal fin X; posterior dorsal fin 12; pectoral fin 12–13; pelvic fin I, 5; anal fin III, 8–9. Origin of anal fin nearly opposite origin of posterior dorsal. Caudal fin truncate. Ctenoid scales with about seven ridges radiating apically.

REMARKS: The Recent species of the genus *Percichthys* are discussed by Eigenmann (1909, p. 284; 1927, p. 61). *P. antiquus* (pl. 7) agrees very closely in observable characters with *P. trucha*, a species that occurs in both Patagonia and Chile. The presence of *P. antiquus* in the fresh-water Tertiary of Brazil indicates that this genus must have had a much greater distribution than it does at the present time. It is also evident that the genus was restricted to fresh water by the Eocene with the discovery of *P. hondoensis* in the Lower Eocene of Patagonia (Schaeffer, 1947).

According to all recent taxonomic treatments of this genus, it should be included in the Serranidae rather than the Percidae. Woodward so placed it in his original description of *P. antiquus* (1898), although he included it in the Percidae later (1901), the family Serranidae not being recognized in the latter work. *Percichthys* bears a close resemblance to the percids, and Jordan (1923) was undoubtedly cognizant of this when he created a separate family, the Percichthyidae, which he considered to be intermediate between the Percidae and Moronidae or white basses. Von Ihering's contention (1898) that *Percichthys* is not a serranid but a cichlid is denied by Eigenmann (1909, p. 336). The cichlids have, among other differences, but one nostril on each side, while serranids, including *Percichthys*, have two.

Although its resemblance to the percids may be due to its generalized percomorph nature, *Percichthys* does appear to bridge the small morphological gap between the percids and serranids in most respects. A comparison of the Eocene Serranidae and Percidae (Schaeffer, 1947) indicates very few, if any, distinguishing differences between these families. The number of anal spines, which has been employed rather arbitrarily to separate the early serranids and percids, is by itself a character of questionable value. The number of vertebrae in *P. antiquus* and the Recent species of this genus is within the Recent percid range of 30 to 48. *P. hondoensis*, however, has 24–26 vertebrae, the principal observable difference between it and *P. antiquus*, but in agreement with the vertebral number for most Eocene perches and basses. One character that favors placing *Percichthys* in the Serranidae is the presence of a serranid-like subocular shelf, observed in a specimen of *P. trucha*, but not recognizable in either fossil species.

The assignment of *Percichthys* to the Serranidae is hence more or less arbitrary, at least as far as the osteological characters are concerned. This fact has been noted by several ichthyologists including Hills (1934, p. 170) in a discussion of the affinities of *Pericalates*. Although *Pericalates* is assigned to the Moronidae, *Pericalates antiquus* from the Paleogene of Australia appears to resemble *Percichthys* very closely. This can only be

considered as further evidence of the merging of the Percidae, Serranidae, Moronidae, and related groups in the early Tertiary.

REFERRED SPECIMENS: A.M.N.H. Nos. 10091–10094.

FAMILY CICHLIDAE

GENUS *AEQUIDENS* EIGENMANN AND BRAY, 1894

Acara HECKEL (in part), 1840, p. 338.

Aequidens EIGENMANN AND BRAY, 1894, p. 616.

GENOTYPE: *Acara tetramerus* Heckel. (For generic diagnosis based on osteological characters, see Regan, 1905, p. 330.)

Aequidens pauloensis,¹ new species

TYPE: A.M.N.H. No. 10095. Nearly complete specimen with dorsal, anal, and tip of caudal fin missing.

HORIZON AND LOCALITY: ?Pliocene beds at Tremembé, São Paulo.

DIAGNOSIS: Length to end of vertebral column about 13.75 cm, greatest depth about 7.5 cm. Skull about one-third total length of body. Dentition as in *A. tetramerus*. Cheek and opercular bones scaled, excepting preopercular. Vertebrae about 26–28: abdominal about 10–12, caudal 16. Dorsal fin with approximately 29 spines and rays; pectoral fin 13–14; pelvic fin I, 5; anal fin III, 8–10. Origin of anal fin opposite posterior third of dorsal. Scales finely ctenoid.

REMARKS: Regan (1905) thoroughly reviewed the osteological characters of *Acara tetramerus* and related species, but did not clear up the taxonomy of *Acara* (see Eigenmann, 1910, p. 470). *A. pauloensis* (pl. 4, fig. 3) agrees with the other species of *Aequidens*, such as *A. tetramerus*, in the relative length of the ascending process of the premaxillary which just extends to the orbit. The total number of vertebrae appears to be the same, although it cannot be definitely determined

¹ From State of São Paulo in which specimen was found.

in the single available specimen. *A. pauloensis* has 16 caudal vertebrae while the other species have but 13. There are approximately 29 spines and rays in the dorsal fin according to a count of the interneurals. This number falls at the extreme upper range among the species of *Aequidens* and approaches the number in the related genus *Astronotus*. Until more and better preserved material is available in which the vertebrae and the spines and rays of the dorsal fin can be accurately counted it would appear advisable to assign *pauloensis* to *Aequidens* rather than to create a new genus.

An indeterminable species of *Acara* has been described by Woodward (1898) from a fragment collected at Taubaté. It agrees in all noted characters with the specimen described above excepting a smaller dorsal fin formula XIV, 8–9. The number of vertebrae in this form is unknown. Woodward (1939) has also described another cichlid, *Macracara prisca*, from presumably early Tertiary beds exposed at Nova York, Maranhão. It differs from the *Aequidens* group in having 36 vertebrae but is otherwise very similar.

The Cichlidae are not known from the Tertiary of North America. Regan (1908) and Myers (1937) are of the opinion that *Priscacara* and *Cockerellites*, considered to be cichlids by Cope, Haseman, and Pearson, are more closely related to the sunfishes, and Romer (1945) has placed them in the Pomacentridae. One genus, *Cichlasoma*, is found in the Miocene of the West Indies and also occurs today in South America. Three genera, two of which are still in existence, are found fossil in Africa. *Palaeochromis* from the Tertiary of North Africa is considered by Sauvage (1907) to be related to *Acara*. Such resemblance, however, is probably due to the generalized cichlid pattern shared by both, which may also account for the resemblance between many of the Recent South American and African cichlids.

DISCUSSION

ANALYSIS OF FOSSIL ASSEMBLAGE

THE FOSSIL ACTINOPTERYGIAN FISHES that have been described from the Cretaceous and Tertiary deposits of Brazil are listed in table 2. Until the ages of the various formations discussed herein are accurately determined, it appears advisable to consider the known actinopterygians together, particularly since there appears to be no sharp faunal break between the Cretaceous and Tertiary, and the position of the Série Alagoas is still questionable.

As in similar faunal assemblages from other parts of the world, this one demonstrates the rise to dominance of the teleosts and, in this case, the introduction into South America of its typical fresh-water fish fauna. The Cretaceous assemblage, while not very diversified, is typical of the period, and, as will be pointed out below, shows a great similarity to another fauna of similar age. With the last occurrence of *Lepidotus* and *Palaeobalistum* in the Upper Cretaceous, the rather meager evidence indicates that the Holostei disappeared from South America. Possibly the amiids persisted into the Tertiary, although the single specimen thus far discovered belonging to this group comes from the Upper Cretaceous.

The Upper and Lower Cretaceous assemblage is made up of holosteans and teleosteans from marine and estuarine beds. Continental Cretaceous deposits are rare in Brazil, if not entirely missing, although they are found in the western part of South America. In any case, teleosts from such beds are likewise rare, and the Brazilian picture further emphasizes Romer's suggestion (1945) that the teleosts very probably had a marine origin.

As stated by Arambourg and Schneegans

(1935), the resemblance between the Cretaceous fauna of Brazil and that of the Gabon Basin in West Africa is very striking. *Diplo-mystus longicostatus* from the Série Baía and *D. goodi* from the Gabon Basin are very similar and, as pointed out earlier, apparently belong to the same phyletic line. The similarity further includes closely related channids, the chirocentrids *Chiromystus* and ?*Chiro-centrites*, *Enchodus*, *Leptolepis*, and a lepidotid with squamation resembling that of *L. mawsoni*. This faunal resemblance, however, does not necessarily imply a close age correlation between the beds in Africa and Brazil. The deposits of the Gabon Basin are considered by the above authors to be Middle Cretaceous (Lower Cenomanian or Albian), while the beds in Brazil yielding this assemblage are considered to represent a much greater portion of the Cretaceous (Middle Albian through the Maestrichtian). Until the age of the formations involved is better understood, the significance of this resemblance, except in a general way, largely remains a moot question.

The questionable early Tertiary deposits in Baía, regarded at present by the Brazilian Survey as possibly Upper Cretaceous in age, contain a fauna that unfortunately offers little assistance in settling this problem, as many of the genera represented are known to occur in formations of both periods. The later Tertiary deposits in São Paulo, possibly Pliocene, are entirely lacustrine-fluvial and contain a fresh-water fauna that is Recent in character, indicating that this assemblage was already in existence by no later than mid-Tertiary time.

THE ORIGIN OF THE SOUTH AMERICAN FRESH-WATER FISH FAUNA

The origin of the fresh-water fish assemblage of South America has been the subject of much speculation that is based, for the most part, on information obtained from studies of the Recent fauna. There has been some consideration of the paleontological

evidence by Haseman, Myers, and Gosline, and these authors are well aware of its importance. As the problem is essentially a historical one, the ultimate solution can be revealed only by paleontological and geological data.

[illegible]

TABLE 2—Continued

	Cretaceous						Tertiary			
	Grupo Ganhamaroba	Série Grajau	Série Araripe	Fomção Almada	Série Bafa	Rio Gramame Limestone	Formação Maria Farinha	Série Alagoas	Nova York, Maranhão	Tabaté and Tremembé, São Paulo
Chirocentridae										
<i>Cladocyclus gardneri</i> Agassiz, 1841			X							
<i>Chiromystus mawsoni</i> Cope, 1885					X					
<i>Chiromystus alagoensis</i> Jordan, 1910								X		
Chanidae										
<i>Dastilbe crandalli</i> Jordan, 1910			X					X		
Clupeidae										
<i>Scombroclupeoides scutata</i> (Woodward, 1908)				X						
<i>Diplomystus longicostatus</i> Cope, 1885					X					
<i>Knightia branneri</i> (Jordan, 1910)								X		
<i>Knightia brasiliensis</i> Woodward, 1939									X	
Stomiatoidea										
Enchodontidae										
<i>Enchodus oliveirai</i> Maury, 1930						X				
<i>Enchodus subequilateralis</i> Cope, 1885						X	X			
<i>Cimolichthys</i> n. sp. Williston, 1902										
OSTARIOPHYSI										
Cyprinoidea										
Characinidae										
<i>Eobrycon avus</i> (Woodward, 1898)										X
<i>Eobrycon branneri</i> Eigenmann, 1929										X
<i>Eobrycon ligniticus</i> (Woodward, 1898)										X
Siluroidea										
Ariidae										
<i>Arius iheringi</i> Woodward, 1898										X
ACANTHOPTERYGII										
Percoidea										
Serranidae										
<i>Percichthys antiquus</i> Woodward, 1898										X
Cichlidae										
<i>Acara</i> sp. Woodward, 1898										X
<i>Aequidens pauloensis</i> , new species										X
<i>Macracara prisca</i> Woodward, 1939									X	

There are probably but four possibilities that might be considered to explain the dispersal of a fresh-water fish fauna into South America (or Africa): (a) by marine radiation, (b) by land bridges, (c) by direct contact of South America and Africa prior to drifting apart, and (d) by Holarctic continental dis-

tribution. It is furthermore probable that the various elements of the fauna employed different or several means of dispersal, although there is no way of demonstrating this at the present time. While each of these alternatives has received much attention, the paleontological evidence that has accumulated in recent

years has not been considered. These data are still very fragmentary, but they do suggest certain conclusions such as the early arrival of the characins and the possible late appearance of the osteoglossids, and they offer a basis for future investigation along possibly less speculative lines.

MARINE DISTRIBUTION

Myers (1938) has analyzed the Recent South American fresh-water fish fauna from the standpoint of its origin. In this connection, he separates all fresh-water fishes into two categories: (1) a primary division consisting of fishes that are always restricted to fresh water, and (2) a secondary division including those fishes that are able to enter the sea for a short period of time. Of the various fishes which he places in each division, only those that have been found as fossils in Brazil will be considered here.

The distinctness of the Recent South American fresh-water fish fauna centers around the presence of characins and cichlids, both also occurring as fossils and Recent types in Africa. The Characidae are placed by Myers in the primary division and the Cichlidae in the secondary. As pointed out in the section on *Eobrycon*, the identification of characins from scales in Upper Cretaceous marine beds in California, Wyoming, and Peru and their presence in lacustrine Eocene beds in France indicate a far wider distribution for this family than has been generally realized. It is therefore within the realm of possibility that the characins were distributed to the continents by way of the sea during the late Mesozoic and were restricted to fresh water by the early Tertiary. It is further possible that the members of this group became extinct in North America and Europe during the Tertiary because of temperature or other environmental changes. While such conclusions can be substantiated only by further discovery, they offer an alternative explanation for the distribution of the characins without the creation of dubious South Atlantic and Antarctic land bridges.

A clue regarding the dispersal of the cichlids is still to be found. As in the case of the characins, the known fossil representatives from South America and Africa are closely related to Recent species, and thus far no

positively recognizable fossil cichlids have been found in North America (the prisca-carids possibly being related to the sunfishes or close to the base of percoid radiation) or Europe. It is interesting to note, however, that Myers places this family in the secondary division, and Dr. C. M. Breder has informed the writer that a species of *Tilapia* lived for a number of years in sea water at the New York Aquarium. Hence a marine dispersal is again a very reasonable possibility, particularly with Simpson's discussion (1939) of the *Galaxias* problem in mind.

The amiids, placed in the primary division, were spread rather widely over the Northern Hemisphere by the beginning of the Cretaceous. As the Jurassic members of this family occur in marine formations, a marine dispersal is a reasonable possibility. It is therefore not particularly surprising that an amiid, *Urocles mawsoni*, should occur in the Série Bafa. It is rather more surprising that amiid remains are not more common in South America and have not been found in Africa.

The siluroid genus *Arius* is semimarine, and the Tertiary *A. iheringi* from the lacustrine-fluvial deposits at Taubaté was probably a landlocked species. The evidence regarding the dispersal of the catfishes is carefully summarized by Gosline (1944) and will not be discussed here. It will suffice to state that Cretaceous siluroids are unknown, and the Tertiary and Recent forms do not offer even a tentative solution to this problem. Gosline suggests, but considers improbable, that the African and the South American catfishes are all descended from the Ariidae.

The presence of the serranid *Percichthys* in the Taubaté deposits, in the Lower Eocene of Patagonia, and at the present time in the streams of Chile and Patagonia suggests that this genus has been restricted to fresh water since the early Tertiary, as has likewise been the Australian *Percalates* (Hills, 1934). The world-wide distribution, by the early Tertiary, of such transitional percoid-serranid types again suggests a marine distribution in the late Mesozoic. It is becoming increasingly evident that the key to fresh-water fish dispersal lies in the Cretaceous. By the beginning of the Tertiary, the various fresh-water groups were restricted to their present habitat and differentiated to almost the same degree as

their Recent descendants. Gosline's studies appear to support this conclusion.

Fossil osteoglossids have thus far not been discovered in South America. They occur possibly as early as the Cretaceous in North America (?*Eurychis*), certainly by the Eocene in both this continent (*Phareodus*) and in North Africa and Europe (*Brychetus*). *Phareodus* is also present in the Oligocene of Australia in a fresh-water deposit (Hills, 1934). Myers places the osteoglossids in his primary division, although the early members of this group again were probably marine, which could account for their very wide dispersal by the Eocene or Oligocene. The resemblance between the recent Australian genus *Scleropages* and *Phareodus* is not surprising, as the latter existed in the fresh-water streams of Australia prior to the isolation of that continent. There are several conceivable explanations for the lack of fossil osteoglossids in South America: first, that they invaded this continent from the sea in the Cretaceous and their remains have as yet not been found in either marine or continental beds, and second, that if they were entirely restricted to fresh water by the Eocene or Oligocene, they were unable to enter South America until the end of the Tertiary when the connection with North America was reestablished. This problem can, again, be solved only by future discovery.

Gosline (1944) has also dwelt upon the problem of the origin of the South American fresh-water fish fauna with particular reference to the derivation of the Ostariophysi. He considers, for instance, the question of salt-water tolerance and the possibility of the Weberian apparatus being particularly suited or evolved for fresh water. Unfortunately, no amount of work on recent members of this order regarding either of these problems can do more than increase or decrease the probability of a marine origin or marine dispersal. The millions of years involved in such a habitus change might very well obscure changes in the histological structure of the kidney, such as the relative number of the glomeruli in fresh- and salt-water types, and also result in many minor changes in the Weberian apparatus.

Regan has stated that the imperfect past history of the Ostariophysi indicates that this

order has never had a greater distribution than at present, and that the fossil types are all related to genera living today. In this connection, the evidence for the Holarctic presence of the characins will be recalled. It is true, however, that the record of ostariophysian evolution is still very fragmentary, and most of the fossil types known are closely related to Recent genera. As pointed out earlier and agreed to by Gosline, the ostariophysids undoubtedly reached South America during the Mesozoic. The scarcity of continental Mesozoic beds in South America might account for our ignorance concerning them during this era, or the scarcity of their remains in Cretaceous marine beds, the period during which they may have evolved, could be another factor. Furthermore, it may prove very difficult or impossible to distinguish the primitive ostariophysids from the clupeid-like fishes of the Mesozoic, a case in point being the possible origin of the Order Ostariophysi from the Jurassic-Cretaceous Lycoperidae. Lastly, Gosline raises the question of why, if the Ostariophysi could cross a marine barrier, they have not been distributed to a greater extent by this means. If further discovery demonstrates that the Ostariophysi had a marine dispersal, the question more or less answers itself, and also a physiological and structural restriction to fresh water by the Eocene would certainly tend to reduce or eliminate marine distribution after that time.

The somewhat scanty evidence here presented would appear to offer an alternative hypothesis for the origin of the South American fresh-water fauna without the necessity of creating a land bridge between that continent and Africa.

LAND BRIDGE DISPERSAL

With no apparent other possibilities, the land bridge hypothesis has been generally proposed as the one credible solution to the problem. That fresh-water fishes are able to migrate across a land bridge is demonstrated by the northward movement of the cichlids into Texas and the characins into New Mexico by way of the Panamanian connection (the possibility that the cichlids and characins once existed in North America and are now restricted, by temperature, to the South-

west must also be considered). A migration of this sort, excluding transportation by birds, cyclonic storms, etc., could be accomplished probably in only two ways, either by stream capture or by passage through the sea from one river mouth to another. The latter method might be employed by fishes of Myer's second division, such as the cichlids. There is evidence, of course, that Recent fresh-water fishes do use both means of extending their distribution. It is logical, therefore, that fishes of this type could cross a land bridge, given enough time, between South America and Africa. The northward dispersal of the characins and cichlids must have occurred in a relatively short period, probably beginning no earlier than the end of the Tertiary when the connection between North and South America was reestablished.

It may hence be concluded that if land bridges did exist, with a series of originally separate drainage systems, the migration of fresh-water fishes could take place across them. But the fact still remains that there is little geological evidence for the past existence of oceanic land bridges (excepting the Siberian-Alaskan bridge), or, for that matter, of the extensive orogenic disturbances of the ocean floor that would be necessary to produce such bridges. To create them with no geological basis, just to satisfy the needs of zoogeographers, though commonly done, seems unsound.

DISTRIBUTION AND CONTINENTAL DRIFT

Although the hypothesis of continental drift has generally fallen into disrepute in recent years, it is interesting to consider the possibilities offered for distribution. According to one theory, South America and Africa started to separate in the early Cretaceous, thus requiring a fresh-water characin exchange by no later than this time. Myers (1938) points out the very interesting fact that none of the five primitive autochthonous African families of fishes (bichirs, pantodonts, phractolaemids, kneriids, and mormyrids) are found in South America. These families, he believes, were present in Africa before the characins, carps,

and cichlids, although their paleontological history is unknown. In any case, it is rather surprising that, with the two continents united according to the above theory, even these more ancient types did not enter South America. As Myers infers (1938, p. 353), however, a filter bridge between the two continents might have excluded them but permitted exchange of the other groups.

HOLARCTIC CONTINENTAL DISTRIBUTION

Finally, a Holarctic continental distribution of the various groups under discussion remains to be considered. In spite of the presence of marine amiids in the Jurassic, it is entirely possible that they were restricted to fresh water in the Northern Hemisphere during the Cretaceous, entering South America by way of the Panamanian bridge before it was cut off. The indication for this is, however, not particularly convincing because of the lack of any positive paleontological evidence. The same sort of reasoning might be developed for the osteoglossids and the characins on the basis of the meager paleontological evidence. The case for the osteoglossids is possibly on a sounder footing with the positive identification of the North American Eocene *Phareodus*, even though this particular genus is apparently not closely related to either *Osteoglossum* or *Arapaima*. Haseman (1912) developed a number of valid arguments against the land bridge theory and in turn supported a northern origin for the South American fresh-water fish fauna. He considered the known paleontological evidence at some length, relying rather heavily on the much-worked Green River fishes. As Myers (1937) has pointed out, however, this fauna does not clearly support a northern origin, and this is particularly true in the case of the cichlids.

The confusing picture presented by the Recent distribution of vertebrates in South America and Africa can, as has been demonstrated in the case of the mammals, be resolved only by paleontological discovery backed by reasonably probable geological evidence.

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