

Article VIII.—A JURASSIC FISH FAUNA FROM WESTERN CUBA, WITH AN ARRANGEMENT OF THE FAMILIES OF HOLOSTEAN GANOID FISHES

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CONTENTS

	PAGE
INTRODUCTION.....	223
ORDER HOLOSTEI.....	224
Pycnodontidæ.....	224
<i>Gyrodus macrophthalmus cubensis</i> , new subspecies.....	224
Eugnathidæ.....	227
<i>Caturus deani</i> , new species.....	227
Pachycormidæ.....	230
<i>Sauropsis</i> (?) <i>woodwardi</i> , new species.....	230
<i>Eugnathides browni</i> , new genus, new species.....	235
ORDER ISOSPONDYLI.....	236
Leptolepidæ.....	236
<i>Leptolepis</i> (?) <i>euspondylus</i> , new species.....	236
AN ARRANGEMENT OF THE FAMILIES OF HOLOSTEAN GANOID FISHES.....	237

INTRODUCTION

During the course of Mr. Barnum Brown's explorations in Cuba (1911–1919) he paid special attention to the Jurassic formations of the western province, Pinar del Rio, studying especially the stratigraphic sequence on the southern flanks of the Sierra de los Organos and making large collections of the ammonites and other invertebrates, which have supplied the means of correlating the horizons of the Cuban Jurassic with those of Europe.¹ The horizons range from the Lower Oölitic upward, through the Oxfordian, Corallian, Kimmeridgian and Portlandian.

The fossil ganoid fishes described below were collected by Mr. Brown in the Viñales section. They are found in black limestone accretions, or nodules, sometimes in association with ammonites. At Mina Constancia they are recorded as from the "Lowest Jurassic" but their relationships seem to be rather with Kimmeridgian forms. The fishes were mostly of relatively large size. First, there was a compressed, deep-bodied fish of the genus *Gyrodus*, a large pycnodont, about a third of a meter in length, with round-topped teeth, probably adapted for crushing

¹Cf. Brown, Barnum, 1919, 'Discovery of the Oxfordian in Western Cuba,' Bull. Geol. Soc. Amer., XXX, p. 152 (abstract).

Brown, Barnum, and O'Connell, Marjorie, 1922, 'Correlation of the Jurassic Formations of Western Cuba,' Bull. Geol. Soc. Amer., XXXIII, Part 3.

mollusc shells. Next there were several predatory forms of the families Eugnathidæ and Pachycormidæ, one of them being perhaps two meters in length. These all evidently belong in the order Holostei or Protospondyli, together with their modern relatives *Lepidosteus* and *Amia*. A much smaller fish, named below *Leptolepis* (?) species, belongs in the order Isospondyli and represents the early and primitive teleosts.

The fish fauna, so far as known, is typically Jurassic in character. The *Gyrodus* seems to be closely related to several of the many species that occur in the Kimmeridgian of Europe. The *Caturus*, *Sauropsis* (?), *Eugnathides*, and *Leptolepis* (?) are related to European forms that range from the Lower Jurassic upward, some even extending into the Wealden.

Perhaps the most interesting result of the present paper is the additional evidence for the very close relationship of the families Eugnathidæ and Pachycormidæ, as already intimated by Dr. Smith Woodward.¹ The writer's views of the inter-relationships of the various families of the order Holostei are indicated at the close of this paper.

ORDER HOLOSTEI (PROTOSPONDYLI)

Pycnodontidæ

***Gyrodus macrophthalmus cubensis*, new subspecies**

TYPE.—Amer. Mus. Cat. Fos. Fishes, No. 7928 (Field number V 1): vomerine and mandibular dentition.

GEOLOGICAL HORIZON AND LOCALITY OF TYPE.—“Basal levels” of the Jurassic, as exposed one kilometer S. E. of San Vicente, Pinar del Rio, Cuba. Of Kimmeridgian age.²

PARATYPE.—Amer. Mus. Cat. Fos. Fishes, No. 7927 (Field number C 1): part of the head with little-worn mandibular teeth and part of the left side of the body showing the scales. From Mina Constancia, six miles N. E. of Viñales.

DESCRIPTION.—Vomerine dentition having the median row equalling or exceeding the two flanking rows in width; crowns of unworn smaller teeth having two concentric mammillate rings and a central papilla; on the larger teeth the papillæ are very numerous and less regular in arrangement, the central papilla and the rings losing their distinctness; all the teeth become smoothly rounded by wear. Body length estimated at about .345 m. Body scales covered with coarse pits, ridges and tubercles, forming a more or less reticular pattern.

The material available indicates that the Cuban species has the central row of vomerine teeth distinctly larger than in *Gyrodus planidens*³ of Kimmeridgian age. The intermediate row of vomerine teeth is

¹Woodward, A. S., 1895, 'Catalogue of the Fossil Fishes in the British Museum,' Part III, p. xvi.

²Brown, B., and O'Connell, M., 1922, p. 648.

³Cf. Woodward, A. S., 1895, 'Cat. Fos. Fishes Brit. Mus.,' Part III, p. 244. (Also contains references to plates in Agassiz and other works examined.)

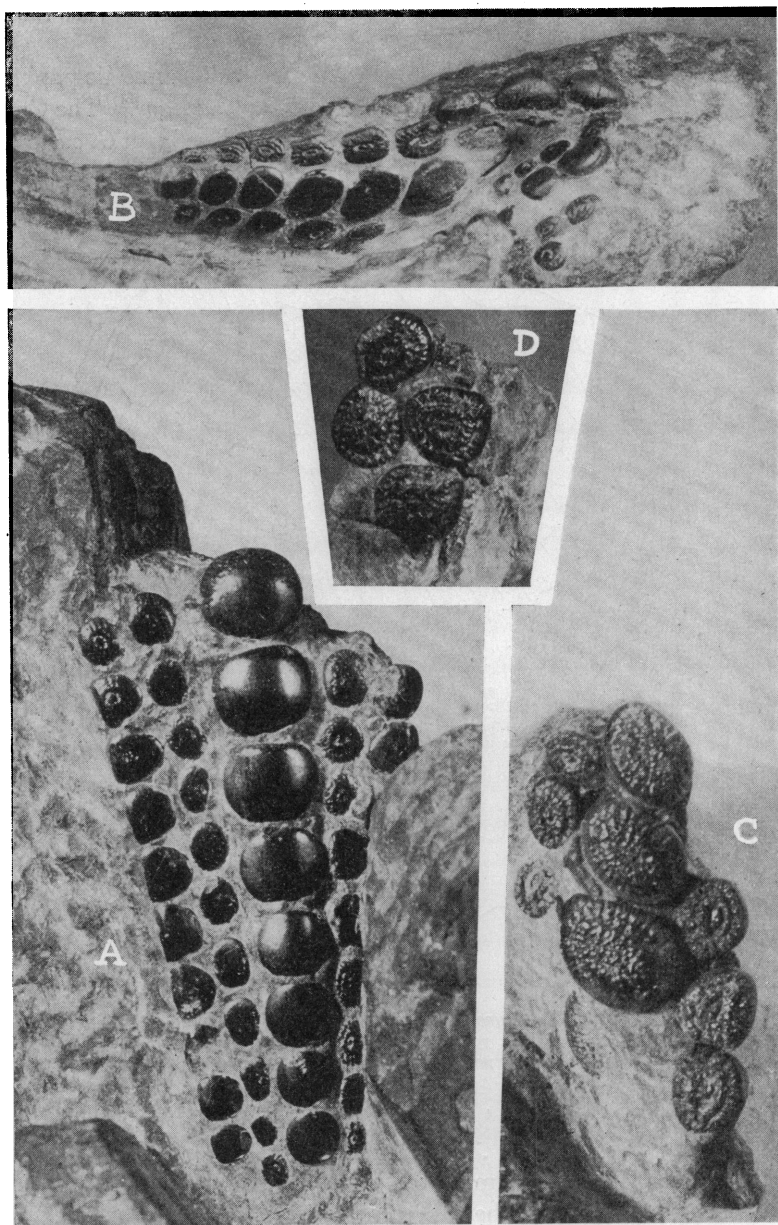


Fig. 1. *Gyrodus macrophthalmus cubensis*.

- A. Vomerine dentition of type (A. M. N. H. No. 7928). $\times 2$.
 B. Mandibular dentition of type, right side, admedial aspect. $\times 2$.
 C. Mandibular teeth of paratype (A. M. N. H. No. 7927) right side. Admedial aspect of upper three rows. $\times 3$.
 D. Vomerine (?) teeth of paratype. The two teeth on the right belong to the marginal row. $\times 3$.

smaller than in the Kimmeridgian *G. coccoderma*.¹ The middle papilla in the teeth is less prominent than in the Neocomian *G. minor*.² The Cuban species appears also to differ from the Lower Kimmeridgian *G. cuvieri*, in which the median vomerine teeth are not quite equal in width to the two flanking series.³ It agrees closely with the description of the Lower

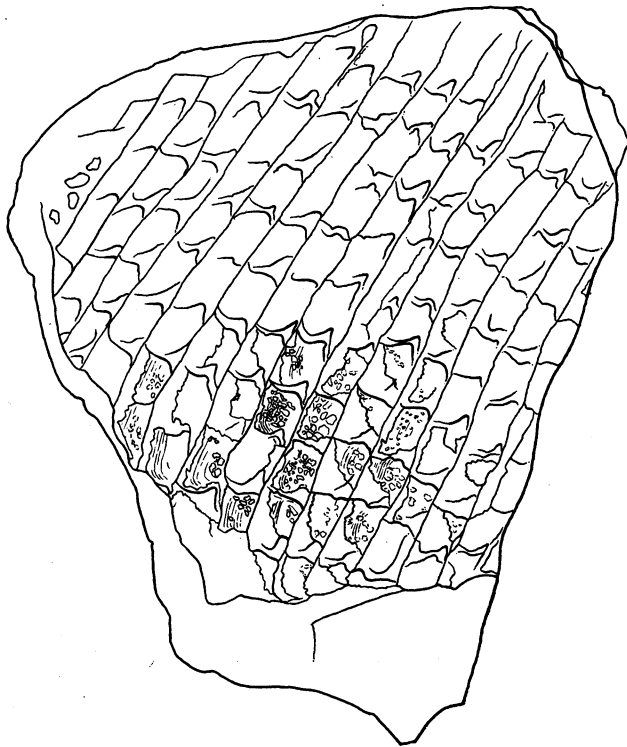


Fig. 2. *Gyrodus macrophthalmus cubensis*.

Part of paratype (A. M. N. H. No. 7927). Fifteen rows of scales covering the lower part of the left surface, extending from just behind the pectoral girdle nearly to the pelvis. $\times \frac{1}{2}$.

Kimmeridgian *G. circularis*⁴ except that it seems to be much smaller in size (estimated body length .345, as compared with 1 m.) It seems to agree with the largest specimens of *G. macrophthalmus* (also Lower Kimmeridgian) in size and in the general characters of the dentition. It is provisionally assigned as a distinct subspecies of *G. macrophthalmus* on

¹Cf. Egerton, Sir P., 1869, Quart. Jour. Geol. Soc., XXV, p. 383, fig. 4.

²Cf. Woodward, A. S., *op. cit.*, p. 242.

³Idem, p. 240.

⁴Idem, p. 238.

account of its wide separation in space from the European form. It may well prove worthy of specific rank when more and better material becomes known.

Eugnathidæ

Caturus deani,¹ new species

TYPE.—A. M. N. H. Cat. Fos. Fishes, No. 7930 (C 28): a crushed head, showing especially the outer aspects of the lower jaw, gular plate and branchiostegals; also the premaxilla, maxilla, vomer, orbit, cheek plates, and opercular region.

GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic” one mile east of Constancia (near Viñales). Probably of Kimmeridgian age.

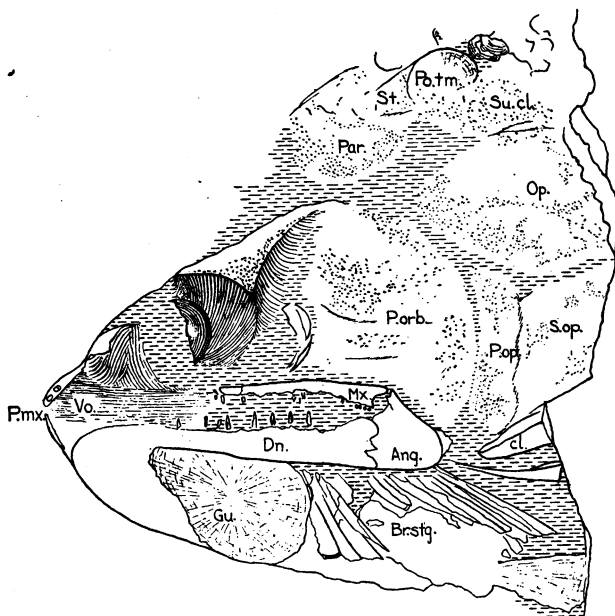


Fig. 3. *Caturus deani*.

Type skull (A. M. N. H. No. 7930). $\times \frac{1}{2}$.

REFERRED SPECIMENS.—A. M. N. H. No. 7931 (C 8): a crushed skull, somewhat larger than the type, from the same locality and horizon; A. M. N. H. No. 7933 (C 14) a crushed fish, showing the dorsal aspect of the fore part of the body. Same locality.

DESCRIPTION.—Size large (possibly .7 m. and upward in total length); length of head from tip of snout to posterior border of operculum about .163 m. Gular plate large (.055 in length). Surface of gular plate ornamented with minute pustules. Length of mandible about .095. Opercular region ornamented with fine irregular

¹Dedicated to my honored preceptor in ichthyology, Professor Bashford Dean.

tubercles and rugæ. Scales (so far as preserved) large, rounded. Maxillary teeth small, slender, numerous, those of the dentary larger, stouter and well spaced, base of teeth not divided. Premaxillary larger than maxillary teeth. Dentary teeth slender, straight, sharply pointed, about 5 mm. in height above the alveolar border, separated from each other by intervals of about $3\frac{1}{2}$ mm.

As this fish is known only from the head region, such generic and specific characters as would be shown in the general form of body, characters of the vertebræ and tail, proportion of head to body, length, form and position of fins, surface characters of scales, etc., are not presented either in the type or in the certainly referred specimens.

The ordinal relationships of the fish, however, are clear. The fact that it belongs in the order Holostei, or Protospondyli, comprising the existing *Amia*, *Lepidosteus*, and their numerous fossil allies, is shown by the presence in the type and referred specimens of the large gular plate and by the fundamental similarity of all parts of the head to that of *Amia*.

Reference of the Cuban fish to the small-mouthed holostean families Pycnodontidæ, Semionotidæ, Macrosemiidæ, is excluded by the large size of its mouth and by the relatively greater anteroposterior length of the whole head, and especially of the postorbital plates. On the other hand, a reference to the long-snouted families, Lepidosteidæ and Aspidorhynchidæ, is excluded by the normal and unspecialized form of its snout and jaws. Of the three remaining families (Amiidæ, Eugnathidæ, Pachycormidæ), the Amiidæ are at once excluded by their shorter jaws, which are more transversely bowed in front, and usually by their very large cycloid scales. The Cuban fossil is undoubtedly nearer to the Eugnathidæ than to the Amiidæ. Within the Eugnathidæ, *Heterolepidotus*¹ is at once distinguished from the present form by its thick rhombic scales and short operculum; *Allolepidotus*² and *Ptycholepis*³ also have thick scales.

It was at first rather difficult to distinguish the type specimen from the genus *Eugnathus*, with which it agrees in the general characters of the jaws and dentition, but the scales present in the type and referred specimens are relatively large and rounded, instead of small and sharply rhombic, the sclerotic is well ossified and the operculum, at least in the referred specimens, appears to be wider than that of *Eugnathus*. From *Osteorhachis macrocephalus*⁴ the Cuban form is distinguished by its more robust jaws, wider operculum, and apparent absence of clustered delicate teeth on the splenial and ectopterygoid (as indicated in referred specimens).

¹Woodward, A. S., *op. cit.*, p. 312.

²*Op. cit.*, p. 315.

³*Op. cit.*, p. 316.

⁴*Op. cit.*, p. 325; also Woodward, A. S., 1895, *Geol. Magazine*, N.S., Dec. IV, II, p. 204 and Pl. VII, fig. 10.

From most of the numerous species of *Caturus* described by Smith Woodward (*op. cit.*), Agassiz,¹ Thiollière,² and others the Cuban fossil differs in its much larger size and in the relative proportions of its jaws and dentition. However, it agrees with *Caturus heterurus*³ in general characters, especially of the dentition, the maxillary teeth being small, slender and in a close series, the premaxillary teeth larger, the dentary series being the largest of all and comprising slender, well-spaced, straight sharply-pointed teeth, with undivided bases.

The fish as a whole is considerably larger than *C. heterurus*, the estimated total length being about 0.70 as compared with 0.45 in the last-named species. The scales also appear to be relatively larger and more rounded. In the type they are seen only from the inner side and the surface ornamentation is not shown. There are at least seventeen branchiostegal rays preserved (of which the anterior one is 5 mm. wide at the median end) but there were probably not less than twenty-four in all.

In the construction of the mandible and in the characters of the dentition this fish is essentially identical, except in minor details, with the type of *Sauropsis* (?) *woodwardi* described below, but the few scales preserved in the type of *Caturus deani* are relatively large and rounded, while those preserved in the type of *Sauropsis* (?) *woodwardi* are small and rhombic in appearance except on the ventral side, where they are much larger. Again, the close agreements of *Caturus deani* with known specimens of *Caturus*, and of *Sauropsis* (?) *woodwardi* with the less specialized genera of the Pachycormidæ (see below, page 234) suggest that these two Cuban forms really belong to distinct genera. At the same time, the Cuban material reinforces the conclusion already suggested by Woodward⁴ that the more primitive Pachycormidæ, such as *Sauropsis*, are only a little more advanced than the more progressive species of *Caturus* of the family Eugnathidæ.

The large scales, very large gular plate, and coarse branchiostegal rays of *Caturus deani*, as well as the rugose ornamentation of the opercular region, thus appear to favor its allocation with the Eugnathidæ rather than with the Pachycormidæ; but the final settlement of this problem requires the examination of specimens that shall reveal the characters of the vertebral column, the form and proportions of the body, and the form and position of the fins.

¹Agassiz, Louis, 1833-1845, 'Poissons Fossiles,' I, p. 194, II, pp. 115-119, 164, 165, 293, 294, Tab. 56, 56a. (For further references to Agassiz's plates see Woodward, as cited below.)

²Thiollière, Victor, 1873, 'Description des Poissons Fossiles provenant des Gisements Coralliens du Jura dans le Bugey,' pp. 17, 18, Pls. XII, XIII.

³Woodward, S. A., *op. cit.*, p. 339.

⁴Idem, p. xvi.

Pachycormidæ (?)**Sauropsis (?) woodwardi,¹ new species**

TYPE.—A. M. N. H. No. 7934 Cat. Fos. Fishes (C 26): crushed head and pectoral region, showing mostly the inner aspects of the skull, jaws, and opercular region.

GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic, 1 mile E. of Constan-
cia. Basal 100 ft. and concretions.” (? Kimmeridgian.)

DESCRIPTION.—Head and dentition of eugnathoid type, except that the oper-
culum is wider (width .042) than deep (depth .035). Size large, length of head from
tip of rostrum to posterior border of operculum about .145. Surface of opercular
region ornamented with fine, irregular tubercles and rugæ. Length of mandible about
.095, depth at posterior end .024. Splenial, a large thin plate bearing at most a single
row of very fine teeth. Scales on fore part of flanks rhombic, small, becoming larger
on ventral surface. Pectoral fins more or less sickle-shaped with about 23 rays which
branch only near the distal end. Small pelvic fins located not far behind pectorals.
Parieto-occipital protuberance not pronounced. Frontals separate.

Comparison with the Genera and Species of Eugnathidæ

This fish differs from *Eugnathus orthostomus*² in its non-rectangular
operculum, which is wider than deep; its scales, though rhombic, are
very small and not strengthened on the inner face with a vertical median
rib; the mandible appears to be deeper anteriorly. From *Eugnathus*
*philpotæ*³ it is distinguished by the much smaller size of the scales and by
the elongate operculum, as well as by the ornamentation of the opercular
region. It differs from *E. minor*⁴ Agassiz in its much greater size, stouter
mandible, wider operculum, and smaller scales. From *E. serratus*⁵ the
species under consideration differs especially in the lesser depth of the
abdominal region. It suggests *Eugnathus altus*⁶ in the small size and
narrowness of the flank scales but differs in the stouter mandible, wider
operculum, and far greater size. *E. hastingiæ*⁷ is a very small fish with
slender jaws; *E. microlepidotus*⁸ has large and very robust teeth on the
dentary bone, of which there is no evidence in the present species. *E.*
*longiserratus*⁹ is a small species with slender jaws, narrow operculum and
relatively larger scales. *E. latimanus*¹⁰ is a small fish with a small short
head.

¹Named in honor of Dr. A. Smith Woodward, whose 'Catalogue of the Fossil Fishes of the British Museum' is the leading modern work on the evolution and taxonomy of the holostean ganoids.

²Woodward, A. S., 'Cat. Fos. Fishes, Brit. Mus.,' III, p. 291. (Also gives references to Agassiz and other literature consulted.)

³Idem, p. 294.

⁴Idem, p. 296.

⁵Idem, p. 298.

⁶Idem, p. 299.

⁷Idem, p. 299.

⁸Idem, p. 300.

⁹Idem, p. 301.

¹⁰Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 302.

From *Heterolepidotus latus*¹ and *H. serrulatus*² the present species is excluded by its much smaller scales and longer head; in *H. typicus*³ the operculum is not so wide. *H. striatus*⁴ is a small Upper Triassic species of robust proportions, opercular bones ornamented with coarse rugæ. *H. cephalus*⁵ (Upper Triassic) is a very small species in which the operculum is much deeper than broad; the remaining species of *Heterolepidotus*, as described by Smith Woodward,⁶ are likewise easily distinguished from the present species.

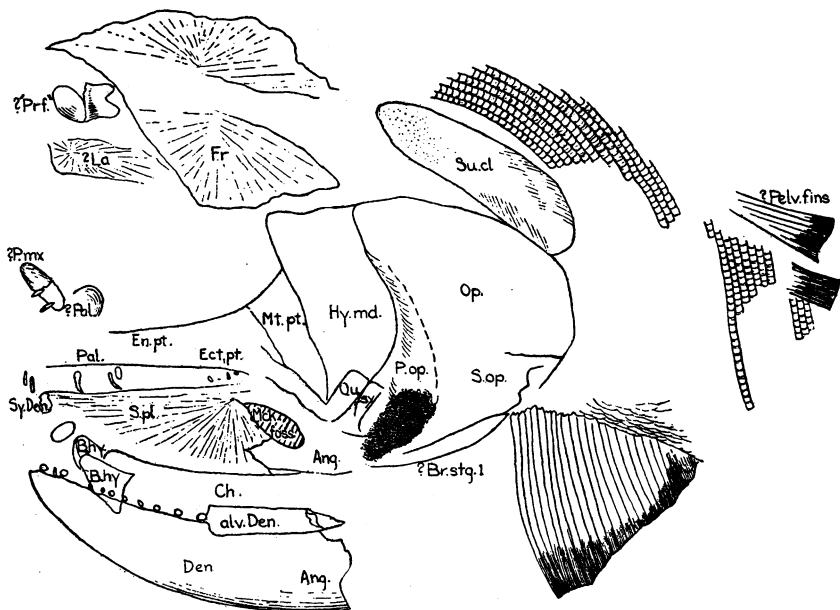


Fig. 4. *Sauropsis* (?) *woodwardi*.

Type, A. M. N. H. No. 7934. $\times \frac{1}{2}$.

Allolepidotus,⁷ an Upper Triassic genus, has a robust form of body and shows no special relationship to *Sauropsis* (?) *woodwardi*.

Ptycholepis,⁸ from the Upper Trias and Lower Lias, has a highly characteristic surface ornamentation of prominent ridges on the head and in the thick scales.

¹Idem, p. 304.

²Idem, p. 307.

³Idem, p. 308.

⁴Idem, p. 311.

⁵Idem, p. 311.

⁶Idem, pp. 312-314.

⁷Idem, p. 315.

⁸Idem, p. 316.

In *Osteorhachis*¹ the operculum is deeper than broad and the scales have a large peg-and-socket articulation, which is not visible in *Sauropsis* (?).

The fish under consideration comes closer to *Caturus*,² but differs from it in having small rhombic scales on the fore part of the flank, the operculum is more elongate anteriorly, the mandible stouter; the pectoral fins have a greater number of rays ($23:14\pm$). More in detail: *C. furcatus*³ has large, very numerous teeth and slender jaws; *C. pachyurus*⁴ is a small species with relatively larger teeth than in the Cuban fish; in *C. velifer*⁵ and *C. drieri*⁶ the teeth are very small and numerous, much more so than in *Sauropsis* (?); *C. velifer*⁷ is nearly related to *C. drieri* and has slender jaws; in *C. angustus*⁸ the head is unknown but the body is much smaller than in *Sauropsis* (?).

*C. heterurus*⁹ comes nearer to *Sauropsis* (?) but has a more slender mandible and fewer rays in the pectoral fin; the operculum also is less elongate. *Caturus latipennis*¹⁰ is closely similar to *C. heterurus*; *C. agassizi* may be the young of the latter (Woodward); in *C. insignis*¹¹ of the Upper Trias the operculum is twice as deep as broad, whereas in *Sauropsis* (?) it is broader than deep. *C. chiotes*¹² has very wide-based, large mandibular teeth, wholly unlike the slender teeth of *Sauropsis* (?); *C. giganteus*¹³ has remarkably large and tumid teeth on the maxilla; *C. suchoides*¹⁴ has the maxilla much like that of *C. giganteus* but less deepened behind, dentary attenuated; teeth indented at base (not so in *Sauropsis* (?); in *C. impar*¹⁵ the maxilla is thick and much arched. *C. purbeckensis*¹⁶ is a very small species in which the external bones are without ornament, the mandible very slender; teeth indented.

The type of *Sauropsis* (?) *woodwardi*, as already noted, agrees with that of *Caturus deani* in the fundamental construction of the mandible and dentition, and even of the skull as a whole. The separation of these two forms is rendered further difficult by the characters of specimen No. 7935 (C 22), in which the detailed construction of the mandible and denti-

¹Idem. pp. 324-326.

²Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 330.

³Idem, p. 332.

⁴Idem, p. 336.

⁵Idem, p. 338.

⁶Idem, p. 337.

⁷Idem, p. 338.

⁸Idem, p. 339.

⁹Idem, p. 339.

¹⁰Idem, p. 342.

¹¹Idem, p. 343.

¹²Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 344.

¹³Idem, p. 346.

¹⁴Idem, p. 346.

¹⁵Idem, p. 347.

¹⁶Idem, p. 348.

tion tend to bridge the differences in the type specimens of *C. deani* and *S. (?) woodwardi*. But, on the other hand, the skull top of the annectent specimen distinctly approaches the primitive pachycormid type as figured by Woodward¹ and tends to reinforce the comparison of *Sauropsis* (?) *woodwardi* with the pachycormid genera *Sauropsis* and *Euthynotus* (see below).

*Callopterus*² of the Kimmeridgian and Wealden is a progressive genus pointing toward the Amiidae; it differs from *Sauropsis* (?) in its deep operculum, shorter jaw and large cycloid scales.

*Eurycormus egertoni*³ equals or exceeds *Sauropsis* (?) in size, but it has large tuberculate scales, longer jaws with more delicate teeth. *E. grandis*⁴ from the Kimmeridge Clay, differs from *Sauropsis* (?) in (a) deeper operculum; (b) pustulate surface of skull; and (c) very numerous fine teeth on maxilla, which is very broad and massive.

Neorhombolepis,⁵ from the Turonian, has a deep head, slender mandible and wide maxilla; the anterior fin ray of the pectoral fin is greatly enlarged and there are only about thirteen rays on the pectoral fin; all conspicuous differences from *Sauropsis* (?) *woodwardi*.

The Cretaceous genus *Lophiostomus*⁶ is a very small fish with a large depressed head and very large jaws.

Comparison with Amiidae

From all the Amiidae except *Liodesmus*, *Sauropsis* (?) *woodwardi* differs in the very small size of the scales which also are not broadly overlapping; the operculum is wider, the mandible less strongly bowed in front and the pelvic fins further forward. *Liodesmus*⁷ is a minute amiid with very small scales. Its head, as figured, is not especially like that of *Sauropsis* (?) *woodwardi*.

Comparison with Pachycormidae

The species under consideration agrees with some of the more primitive Pachycormidae in having very small scales, pelvics far forward, wide operculum and cheek plates.

From *Hypsocormus*⁸ and *Protosphyræna*⁹ it is at once excluded by the absence of an elongate rostrum and greatly enlarged vomerine tusks,

¹*Op. cit.*, Pl. XIV, fig. 1.

²Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.', III, p. 315; see also Traquair, 1911, 'Les Poissons Wealdiens de Bernissart,' Mém. Mus. Roy. d'Hist. Nat. de Belgique, VI.

³Woodward, A. S., *op. cit.*, p. 352; see also Egerton, Sir P., 'Figs. and Descript. Brit. Organic Remains,' Dec. IX, Mem. Geol. Surv., No. 10, Pl. x.

⁴Woodward, A. S., 1890, Geol. Mag., Dec. III, VII, p. 289, Pl. x, figs. 1-8.

⁵Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.', III, p. 355.

⁶*Idem*, p. 358.

⁷Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.', III, p. 361.

⁸*Idem*, p. 390.

⁹*Idem*, p. 399.

as well as by the form of the mandible and dentition, greater number of rays on the pectoral fin, etc.

It differs from *Pachycormus*¹ especially in having a smaller median eminence on the back of the skull top, in the greater depth and stoutness of the mandible, and in the presence of pelvic fins.

From *Asthenocormus*² it is excluded by its far smaller size, by the presence of minute tubercles and rugæ on the opercular region, and by the narrowness of the flank scales.

The type of *Prosauropsis elongatus*³ from the Upper Lias of Yonne, France, distinctly resembles our fish in its very small scales and in the pectoral fin, which has about thirty rays, unsegmented, and branching only near the border. Nothing is said as to the teeth, but the maxilla is represented in Sauvage's plate as if it were provided with extremely delicate teeth, whereas in our fish there are fair-sized conical teeth preserved on the maxilla and similar but more widely spaced teeth on the dentary; the jaw also in *Prosauropsis* appears to be straighter and less curved along its lower border.

The Cuban fish differs from the Upper Liassic genus *Euthynotus*⁴ in its larger size, but shows a fundamental identity in the construction of the jaws and dentition. The principal generic character of *Euthynotus* is the presence of well-developed hypo- and pleuro-centra, surrounding the notochord. As the type of *Sauropsis* (?) *woodwardi* does not show the slightest indications of vertebral rings or half rings, it seems probable that there were no ossifications in the sheath of the notochord.

On the whole, the nearest resemblances of the Cuban fish appear to be with *Sauropsis* Agassiz as defined by Smith Woodward.⁵ At least, it appears to agree with it in all the following generic characters: "Trunk elongate-fusiform, laterally compressed [a fair inference from the shape of the head]. Head relatively large, and snout not produced; marginal teeth well spaced. No ossifications in sheath of noto-chord. . . Pectoral fins large and sickle-shaped, the rays only branching and articulated at the extreme end; pelvic fins small. . . Scales minute, those of the ventral aspect much broader than deep. . ." The remaining seven generic characters of *Sauropsis*, as given by Woodward, are not revealed in the Cuban material.

Sauropsis (?) *woodwardi* differs from *S. longimanus* Agassiz in its much larger size, the length of the head with opercular apparatus being

¹Idem, p. 380.

²Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 380.

³Idem, p. 376; see also Sauvage, H. E., 1894, Bull. Soc. sci. hist. et nat. Yonne, XLVIII, Pl. I.

⁴Woodward, *op. cit.*, p. 377.

⁵*Op. cit.*, p. 375.

about .140, as compared with about .075 in the latter. It approaches *S. latus* Agassiz¹ in the size of the head but in the latter the pelvic fins arise slightly nearer to the anals than to the pectorals, while in the Cuban fossil, as preserved, they lie near the pectorals.

Conclusion

More and better preserved material may conceivably prove that the marked difference in the appearance of the scales between the types of *Caturus deani* and *Sauropsis* (?) *woodwardi* is due to different accidents of preservation or to the scales being shown in different aspects.² In that event the relationship between the two forms may even amount to identity, especially in view of the annectant characters of a certain specimen mentioned above (A. M. N. H. No. 7935 (C 22)). But meanwhile the differences in the form of the scales in the two types is an objective fact which repeated and critical examination serves only to throw into clearer relief. To describe *Caturus deani* and *Sauropsis* (?) *woodwardi* under a single specific name on the basis of present material would hardly conduce to clearness, since the characters of such a supposed species would be drawn from two lots of material which present either non-homologous parts, or different aspects of homologous parts, or apparently real differences in homologous parts.

In any event, the present material again emphasizes the extremely close relationship of the families Eugnathidæ and Pachycormidæ.

Eugnathides browni,³ new genus and species

TYPE.—A. M. N. H. No. 7937 (C 21): a crushed head, showing parts of the mandible, maxilla, hyomandibula, operculum, pectoral girdle, and fin, with a patch of the scalcation behind the pectoral girdle.

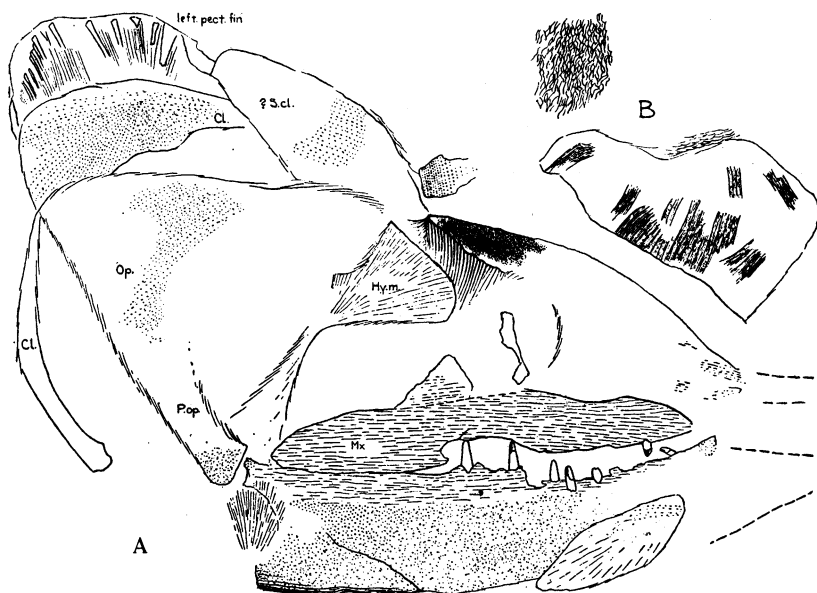
GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic” (? Kimmeridgian), one mile east of Constanica.

DESCRIPTION.—Size very large. Length of head from operculum to tip of snout estimated at .300-. Head and dentition of primitive pachycormid type; mandible relatively stout, the depth of mandible below posterior end of maxilla being .052. Teeth on dentary close-set, stout, conical, slightly incurved, not divided at base; at least 4 mm. wide at base. Hyomandibular large, directed backward. Pectoral fins with very finely divided rays. Scales very small. Surface of mandible ornamented with minute pustules mostly arranged in rows, which tend to pass into fibrous bony tissue.

¹Cf. Woodward, *op. cit.*, p. 376.

²Woodward (*op. cit.*, p. 382) has indeed noted that in the genus *Pachycormus*, “the apparent size of the scales differs greatly according to the degree and manner in which they are displaced.” But in the type of *Sauropsis* (?) *woodwardi* the scales of the fore part of the body are not displaced, although seen mostly from the inner side.

³Named in honor of Barnum Brown, in recognition of his distinguished services to vertebrate paleontology.

Fig. 5. *Eugnathides browni*.

A. Type skull (A. M. N. H. No. 7937).

B. Portion of right pectoral fin and sculation. $\times \frac{1}{2}$.

This large predatory fish is distinguished from *Asthenocormus titan-ius*¹ from the Lithographic Stone of Bavaria, by the presence of minute pustules on the surface (in *Asthenocormus* the surface is described as "fibrous") and by its larger teeth, which in the latter genus are "minute."

It approaches *Sauropsis* (?) *woodwardi* in the very small size of the scales, delicately branched pectoral fin rays and general form of head, but differs apparently in the relatively stouter mandible and in the surface ornamentation, which is more fibrous, with the minute pustules arranged in lines rather than in rugæ.

ORDER ISOSPONDYLI

Leptolepidæ

Leptolepis (?) *euspondylus*, new species

TYPE.—A. M. N. H. No. 7939 (C 11): consisting of a crushed head and pectoral region showing several vertebræ, and some slender ribs.

GEOLOGICAL HORIZON AND LOCALITY.—"Mina Constancia, B." (? Kimmeridgian.)

¹Cf. Woodward, A. S., *op. cit.*, p. 380.

DESCRIPTION.—Notochord persistent, centra consisting of gently constricted cylinders without median lateral ridges. Average length of centra near head 3.8 mm. Ribs slender. Pelvic fins abdominal. Head small.

Relationship with the typical holostean ganoids is definitely excluded by the complete, undivided form of the centra. Relationship with the Oligopleuridæ is excluded by the fact that the vertebræ are not checker-like and the head is small. Relationship with the isospondylous genera *Leptolepis* and *Æthalion* is strongly suggested by the form of the



Fig. 6. *Leptolepis* (?) *euspondylus*.

Type (A. M. N. H. No. 7939), showing outline of skull, ceratohyal, vertebræ, neural arches and ribs. $\times 1$.

head, vertebræ, and ribs. The pelvic fins appear to be farther forward than in *Leptolepis*, while reference to *Æthalion* and *Thrissops* is excluded by the lack of median lateral ridges on the vertebræ. Thus the type specimen very possibly represents a new genus, but, as it reveals so few diagnostic characters, it seems better to refer it provisionally to *Leptolepis*.

AN ARRANGEMENT OF THE FAMILIES OF HOLOSTEAN GANOID FISHES

The evolution and inter-relationships of the families of holostean or protospondylous fishes were so thoroughly considered by Dr. A. S. Woodward in 1895¹ that the passing years have, for the most part, brought only confirmatory evidence to his conclusions. In the arrange-

¹Woodward, A. S., 1895, 'Catalogue of the Fossil Fishes of the British Museum (Natural History),' Introduction to III.

ment of these families submitted below I revise and extend my earlier attempt to summarize the main lines of cleavage and adaptive radiation.¹ As the currently recognized families are of unequal phylogenetic value, some being much more nearly related among themselves than to others, an attempt is made to express these relationships by grouping the families into superfamilies. This very convenient taxonomic method was used extensively by the late Theodore Gill, but its advantages seem to have been overlooked by most ichthyologists.

Superclass OSTEICHTHYES

Class Actinopterygii

Order HOLOSTEI

SEMIONOTOIDEA

Semionotidae

Pycnodontidae

Lepidosteidae

AMIOIDEA

Macrosemiidae

Eugnathidae

Amiidae

Pachycormidae

Order ISOSPONDYLI

PHOLIDOPHOROIDEA

Pholidophoridae

Leptolepididae

Oligopleuridae

Inc. Sedis

Aspidorhynchidae

At the outset we are confronted by the marked difference between English and American systems in the value assigned to the term "order." The system at present adopted by Dr. Smith Woodward sweeps all the hosts of actinopterygian fishes from *Cheirolepis* to *Mola* into a single "order," Actinopterygii, which by Americans is divided into a long series of orders and suborders. As I tried to show in an earlier paper,² the practical mnemonic value of bringing the "families" together into larger groups, in accordance with their inferred degree of relationships, seems to counterbalance the objection that, when the families are so grouped into superfamilies and orders, it is often difficult to construct definitions of the larger group which shall be free of exceptions. One way to define one's concept of a group is to list the forms referred to it,

¹Gregory, W. K., 1907, 'The Orders of Teleostomous Fishes,' Ann. N. Y. Acad. Sci., XVIII, Part 2, No. 3, pp. 437-508.

²*Op. cit.*, pp. 437-445.

to state the characters of its more primitive members or of the ancestral forms, to suggest the lines of evolution with reference to conspicuous characters, and to sketch the extreme specializations.

The order Holostei, or Protospondyli, as here limited, starts with *Acentrophorus* of the Permian, which seems to be a forerunner of the better known *Semionotus* of the Trias. As shown by Smith Woodward, these fishes differ from the earlier Chondrostei especially in the abbreviation of the heterocercal into a semi-heterocercal tail, in the loss or absence of "infraclavicles" (clavicles), in the reduction of the pelvic basals to a single piece, and in the equality in number of the dermal rays of the dorsal and anal fins to their endoskeletal supporting elements. The notochord is persistent, the scales rhombic and heavily coated with ganoin; median fins with large fulcra.

This "order" very early divides into two main groups, called here the Semionotoidea and the Amioidea, although one family, the Macrosemiidae, is almost intermediate between the two. A third group, here called the Pholidophoroidea, represents on the whole a distinctly higher grade of organization than either of the others and may best be regarded as a primitive division of the teleostean order Isospondyli, in which even the earliest known forms have an externally homocercal tail, reduced fin-fulcra, and no "splenial" (coronoid) in the mandible.

Among the Semionotidae the oldest form, *Acentrophorus* of the Permian, has a fusiform body with the dorsal fin short and opposed to the space between the pelvic pair and the anal. In *Semionotus* and more advanced genera the body becomes deeper, the dorsal fin lengthens and tends to shift to the posterior slope of the back. The mouth is small, and the suspensorium (hyomandibular) inclined forward. The teeth are at first all styliform but in the more specialized *Lepidotus* those on the roof of the mouth and inner sides of the jaw become flat-topped and tritoral. Finally, the trunk becomes compressed and very deeply fusiform (*Dapedius*) to cycloidal, with protuberant abdomen (*Tetragonolepis*). Range: Permian (*Acentrophorus*) to Upper Jurassic (certain species of *Lepidotus*).

In all the Semionotidae the dermal plates on the side of the head are arranged in concentric series, the first consisting of a row of small circumorbital plates (homologous with the "suborbitals" of Teleosts); behind this is a row of postorbitals ("suborbitals"); the preoperculum and angular form a third curved series; the "supratemporal" operculum, suboperculum, interoperculum, and branchiostegals constitute a fourth, and the post-temporal, supracleithrum, and cleithrum a fifth. While

there is reason to believe that this arrangement is primitive for the whole order, it becomes widely modified in specialized forms.

Remnants of it persist in the Pycnodontidæ, which, as Woodward has shown,¹ are probably "merely extreme members of the modified series of deep-bodied Protospondyli which begins with *Dapedius*," although no real intermediate forms connecting the two families are known. Paralleling in body form the chætodonts, the platysomids and other deep-bodied, small-mouthed fishes, their most conspicuous specialization is the development of a remarkable dental pavement adapted for crushing perhaps small ammonites and other molluscs. The tritoral round-topped teeth are arranged on the vomers in beautifully spaced rows that converge toward the front and are opposed by alternating rows on the inner sides of the lower jaw. In the presumably more primitive species the median row of vomerine teeth do not greatly exceed the flanking rows in width, as they do in the later and more specialized Cretaceous types.

The Eocene to Recent Lepidosteidæ, as suggested by Goodrich,² appear to be long-bodied offshoots of the Semionotidæ, which have become secondarily predatory and pike-like. They retain much of the primitive semionotid heritage, especially the forwardly-inclined hyomandibular, the circumorbital plates, the very heavy rhombic ganoid scales, the abbreviate heterocercal tail, and the fin fulcra, as well as other points stressed by Goodrich. They even resemble *Lepidotus* in the loss of a gular plate, although they differ from it in the reduction of the preoperculum and in the concomitant enlargement and substitution for it of the interoperculum. The presence of well-ossified opisthocœlous centra in the Eocene to Recent Lepidosteidæ is no bar to relationship with Triassic semionotids in which the chorda was still present. The Lepidosteidæ differ widely from the amioid family Eugnathidæ in skull characters and still more widely from the Aspidorhynchidæ. One can hardly see why they were ever bracketed with the latter in the highly unnatural "Suborder Aetheospondyli," from which they differ in almost every character except those common to other long-bodied, pike-like forms.

The second superfamily, Amioidea, begins with the Upper Triassic to Cretaceous family Macrosemiidæ. These almost divide the differences between the Semionotoidea and the Amioidea, sharing with the former the forwardly-directed suspensorium, although the mouth is

¹*Op. cit.*, p. xii.

²Goodrich, E. S., 1909, in Lankester's 'Treatise on Zoology,' Part IX, pp. 335, 342-344.

distinctly larger and the body more elongate, as in the Amioidea. In this family the dorsal fin becomes elongate and tends to divide into two, the eye is displaced backward and upward with consequent reduction of the cheek plates, and the ring vertebrae when present often show the alternating pleuro- and hypo-centra that are further developed in the more typical Amioidea. The most central family of the latter is the Eugnathidae, which are strongly swimming predatory fishes with large mouths, mostly backwardly-inclined suspensorium and sharp teeth on the outer borders of the mouth. With the backward inclination of the hyomandibular the rows of plates behind the orbits are no longer symmetrically arranged; two of the postorbitals become greatly enlarged and partly overspread the preoperculum. The gular plate is large and conspicuous. In the more primitive members the scales are thick and rhombic, in the more advanced they become thin and deeply overlapping. The vertebrae are either unossified or in the form of separate pleuro- and hypo-centra, sometimes fused into rings, rarely in the form of solid discs.

The Pachycormiidae are advanced to highly specialized derivatives of the Eugnathidae, forshadowing some of the swifter teleosts of later times and finally giving rise to the long-beaked *Protosphyraena*.

The Amiidae are long-bodied fishes with the scales usually thin, deeply imbricating and the caudal fin is usually rounded. *Liodesmus* connects them with the Eugnathidae.¹

The third group, here called the Pholidophoroidea, is referred to the order Isospondyli.

The most primitive family, the Pholodophoridae, ranges from the Trias to the Upper Jurassic. The earlier forms resemble the primitive holostean ganoids in their scales, which, however, are overlapping and often have the hinder margin rounded. They differ from the ganoids especially in the loss of the splenial from the mandible. The mandibular suspensorium is nearly vertical or inclined forwards, but the gape of the mouth is fairly wide and often directed somewhat upward. The teeth are small and conical. The premaxillae are small, the maxillae large, loosely attached and with two supra-maxillary plates, as in the Leptolepidae,² Clupeidae, etc. The vertebral centra never advance beyond the annular stage. The tail, although externally homocercal, is not supported by expanded hypural bones (= haemal arches).

The Jurassic Leptolepidae are the earliest known true teleosts, with thin cycloid scales, vertebral centra nearly complete, no fin fulcrum, inter-

¹Woodward, *op. cit.*, p. 360.

²Woodward, *op. cit.*, p. 446.

muscular bones present, and head and jaws remarkably like those of primitive Clupeidæ. The homocercal tail sometimes develops hypural bones of primitive teleost type (cf. Woodward, *op. cit.*, Pl. xiv, fig. 7).

The Upper Jurassic and Cretaceous Oligopleuridæ resemble the Amiidæ in their large jaws and large rounded scales, but Woodward (*op. cit.*, p. xx) notes that they differ from the Amiidæ in their completely ossified vertebral centra, which never exhibit alternating pleuro- and hypo-central discs (except on the first vertebra); the mandible appears to lack splenial and coronoid elements and the maxilla bears two supra-maxillary bones " which are arranged like those of Pholidophorus and the Clupeoids" (Woodward, *op. cit.*, p. 492).

The Jurassic and Cretaceous Aspidorhynchidæ were provisionally grouped by Woodward, with the Lepidosteidæ but later authorities (Goodrich, 1909, p. 344, Abel, 1919, p. 212) suggest that they are a long-bodied, long-beaked off-shoot of the Pholidophoridæ. They resemble the latter in their deepened flank scales and homocercal tail and in a few other characters but they retain the ganoidean splenial which is lost in the Pholidophoridæ and related families. Their skull, while more or less ganoid in character, shows no special resemblance to any particular family and the presence and homology of the presymphysial bone of the mandible seems difficult to account for. They are practically *Incertæ Sedis*.