Cretaceous Fishes from Bolivia, with Comments on Pristid Evolution

BY BOBB SCHAEFFER[1]

In connection with a current investigation of the Mesozoic rock sequence in central Bolivia, Dr. Aniello Russo of the Yacimientos Petroliferos Fiscales Bolivianos collected vertebrate remains at various localities in a unit recently designated as the El Molino Formation. These remains, which include several kinds of fishes and a turtle, were sent to me for identification and possible age determination by Prof. Leonardo Branisa of the Departamento Nacional de Geología.

I am indebted to Professor Branisa for presenting this collection to the American Museum and for furnishing data on the stratigraphic occurrence. Dr. H. J. Harrington of the Tennessee Overseas Company has generously provided a critical summary of the pertinent stratigraphy. Mr. Charles C. Smith of Houston, Texas, and Dr. Nicholas Hotton of the United States National Museum, Smithsonian Institution, have kindly lent specimens of *Onchopristis dunklei*, and Drs. C. L. McNulty, Jr., and B. H. Slaughter have permitted me to examine their manuscript on this species. Dr. Richard Estes has furnished information on the *Rhombodus-Myledaphus* complex. Dr. J. A. F. Garrick and Dr. D. H. Davies have supplied helpful data on the habits and distribution of the sawfish and sawshark. Dr. M. L. Moss has aided in the interpretation of pristid rostral tooth histology.

The drawings were made by Mr. Michael Insinna, and the photographs were taken by Mr. Chester Tarka.

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GEOLOGIC OCCURRENCE

The post-Paleozoic stratigraphy of Bolivia and adjacent parts of Argentina and Peru has been debated for more than 50 years. The correlation of numerous isolated sequences usually regarded as Cretaceous, and the exact ages of their stratigraphic units, are still not entirely resolved. Because of the many complications involved, the following summary is mostly confined to the rock units in central Bolivia.

In 1904 Steinmann (*in* Steinmann, Hoek, and Bistram) proposed the name "Puca Formation" for thick sequences of predominantly clastic rocks with limestone intercalations exposed at various places in the Central Cordilleras of Bolivia and southern Peru. He considered the Puca to be a northern extension of the Formación Petrolífera of northern Argentina. Later, Bonarelli (1921) subdivided the Formación Petrolífera (called by him the "Sistema de Salta") into the Areniscas Inferiores, the Margas Multicolores (including the Horizonte Calcáreo-Dolomítico), and the Areniscas Superiores. In Bolivia, Schlagintweit (1941) recognized eight units in the classical section of the Puca Formation in the Miraflores Syncline northwest of Potosí. He regarded his Group 3, the Miraflores Limestone, as equivalent to the Horizonte Calcáreo-Dolomítico. This correlation, however, has been the subject of much controversy. The gastropods and echinoids from the Miraflores are generally considered to be Cretaceous, but different workers have regarded the gastropods of the Horizonte Calcáreo-Dolomítico either as Upper Triassic or as Cretaceous (see Harrington, 1962, p. 1800).

Ahlfeld and Braniša (1960), following the terminology of the petroleum geologists, referred to Schlagintweit's Group 1 in the Miraflores Syncline as the Torotoro Sandstone and regarded this unit as equivalent to the Areniscas Inferiores. Certain succeeding groups (presumably Groups 2 through 7) were designated as the Suticollo Formation which was considered to be the same as the Margas Multicolores (again including the Horizonte Calcáreo-Dolomítico). The upper group (8) was excluded from the Suticollo and regarded as equivalent to the Areniscas Superiores. Finally, in 1962, Lohmann and Braniša completely revised the stratigraphic nomenclature for the "Puca" sequence in the Miraflores Syncline on the basis of Schlagintweit's groups, as follows:

> Group 1.....Arenisca La Puerto
> Group 2.....Formación Tarapaya
> Group 3.....Caliza Miraflores Steinmann
> Group 4.....Formación Aroifilla
> Group 5.....Formación Chaunaca
> Group 6.....Formación El Molino

Group 7.....Formación Santa Lucía
Group 8.....Formación Cayara

The "Caliza Miraflores Steinmann" is considered to be Aptian-Albian and the Formación El Molino probably Turonian-Senonian. The Horizonte Calcáreo-Dolomítico is presently correlated with the El Molino on the common occurrence of the calcareous alga *Pucalithus*, rather than with the Miraflores Limestone.

The Formación El Molino, in which all the fish remains were found (L. Braniša, personal communication), is 207 meters thick at the type section on the El Molino farm southwest of Aroifilla and northwest of Potosí (see map, Ahlfeld and Braniša, 1960, p. 113). It consists of a basal white calcareous sandstone overlain by alternating layers of oölitic limestone and marl, succeeded by clays with limestone intercalations at the top.

The El Molino, as defined above, has been recognized in a number of the "Puca" synclines in central Bolivia. At the village of Cayara[1] (on the west limb of the Miraflores syncline), 35 kilometers west of Potosí, the El Molino includes two thin shale layers with fish remains, the lower one containing a clupeid fish. An exposure of oölitic limestone at Leñas, northwest of Potosí on the highway to Challapata, has yielded a distinctive median tuberculated plate that is probably piscine. Turtle fragments are locally abundant in a sandstone outcrop near Vila Vila, southeast of Challapata. At La Cabaña, on the Cochabama-Oruro highway, a thin bone bed is exposed, with fish fragments and gastropods. A "Puca" syncline at Torotoro, about 162 kilometers due north of Potosí, includes a bone bed at the base of the El Molino that contains teeth of a new genus of sawfish, as well as several types of ray teeth.

SYSTEMATIC DESCRIPTIONS

PRISTID TEETH FROM THE EL MOLINO FORMATION

FAMILY PRISTIDAE

SUBFAMILY GANOPRISTINAE

PUCAPRISTIS, NEW GENUS

GENERIC DIAGNOSIS: A genus distinguished from other genera in the family Pristidae, subfamily Ganopristinae, by the following characters

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[1] Most of the localities mentioned here are shown on the maps in Ahlfeld and Braniša (1960).
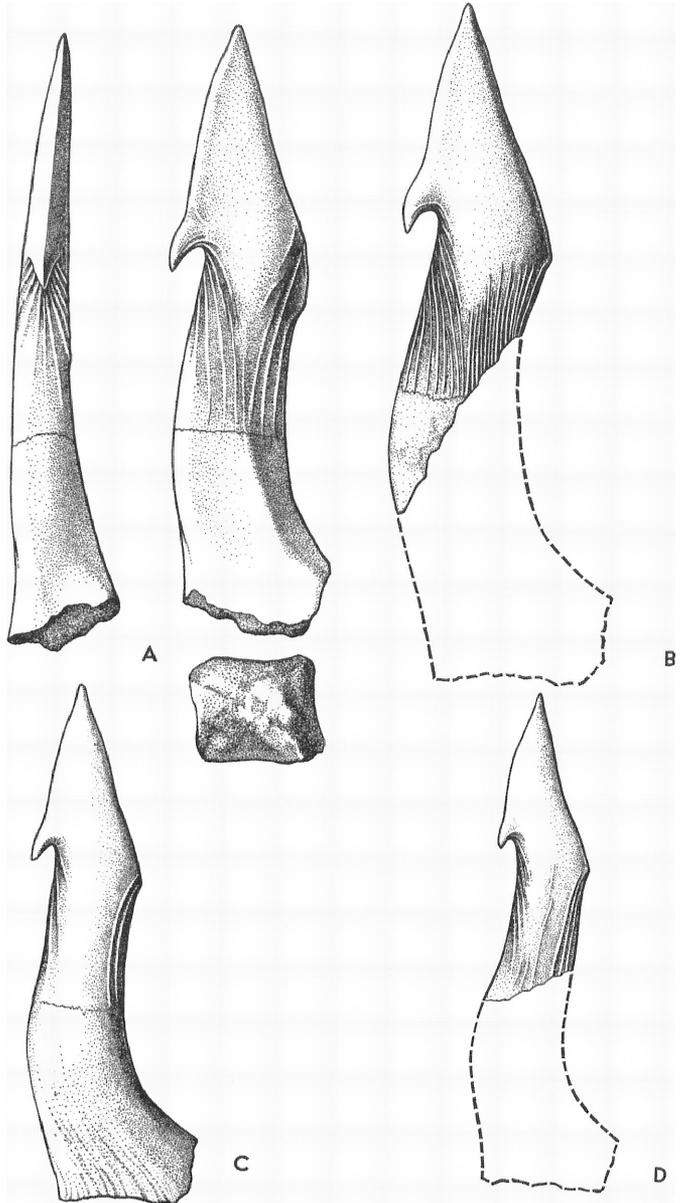
FIG. 1. *Pucapristis branisi*, rostral teeth. A. A.M.N.H. No. 8678, type specimen in posterior, side, and proximal views. B. A.M.N.H. No. 8681, largest specimen in series; note strong enamel ribbing. C. A.M.N.H. No. 8680. D. A.M.N.H. No. 8679, smallest specimen, with nearly complete crown. All ×2.

of the rostral teeth: Crown bowed posteriorly, tapering to sharp point distally, compressed dorsoventrally. Apex of crown with nearly straight anterior border and with a single recurved barb on the posterior border. Crown composed of vertical, anastomosing, dentinal osteons, covered superficially by pallial dentine and enamel. Enamel ribbed proximally. Base slightly expanded, without longitudinal furrows or proximal indentation, composed of vascular bone.

GENOTYPE: *Pucapristis branisi*, new genus and species.

Pucapristis branisi, new genus and species

HORIZON AND LOCALITY: Bone bed in the El Molino Formation, Upper Cretaceous, Torotoro, northeast of Potosí, central Bolivia.

SPECIFIC DIAGNOSIS: Same as for genus.

TYPE: A.M.N.H. No. 8678, complete rostral tooth.

REFERRED SPECIMENS: The available sample includes another complete specimen (A.M.N.H. No. 8680) and fragments of eight additional ones.

DISCUSSION: Although the microstructure of the dentine in the rostral teeth of *Pucapristis* indicates affinity with the *Onchosaurus*-like ganopristines, the external form of these teeth is more suggestive of the *Onchopristis* type. The enamel-covered crown extends to the base, and there is no enamel-free peduncular portion as in *Onchosaurus*. The recurved barb and the ribbing on the enamel are also much like these characters in *Onchopristis numidus* (Stromer, 1917). The shape of the crown apex, with its straight anterior border, and the posterior bowing of the crown proximal to the apex are, however, distinctive features of *Pucapristis*. The teeth appear to have a nearly constant shape regardless of size, and there is not more than one barb. In *O. numidus* there is considerable variation in the shape, curvature, and number of barbs, perhaps related to their size and position on the rostrum (Stromer, *ibid.*, pl. 1).

The crown of the *Pucapristis* rostral tooth is composed of mostly vertical, anastomosing, dentinal osteons, with thin but distinct intervascular bony trabecles. The osteodentine core is surrounded by a thin layer of pallial dentine and a superficial layer of enamel. The bony tissue forming the elongated base is richly supplied with vascular canals. There is no evidence that dentine is present in the basal tissue, and it cannot be regarded as convoluted osteodentine.

The osteodentine-bone transition occurs at the level where the outer pallial dentine plus enamel terminate. This level represents the limit of the internal enamel epithelium which surrounds the crown of the de-
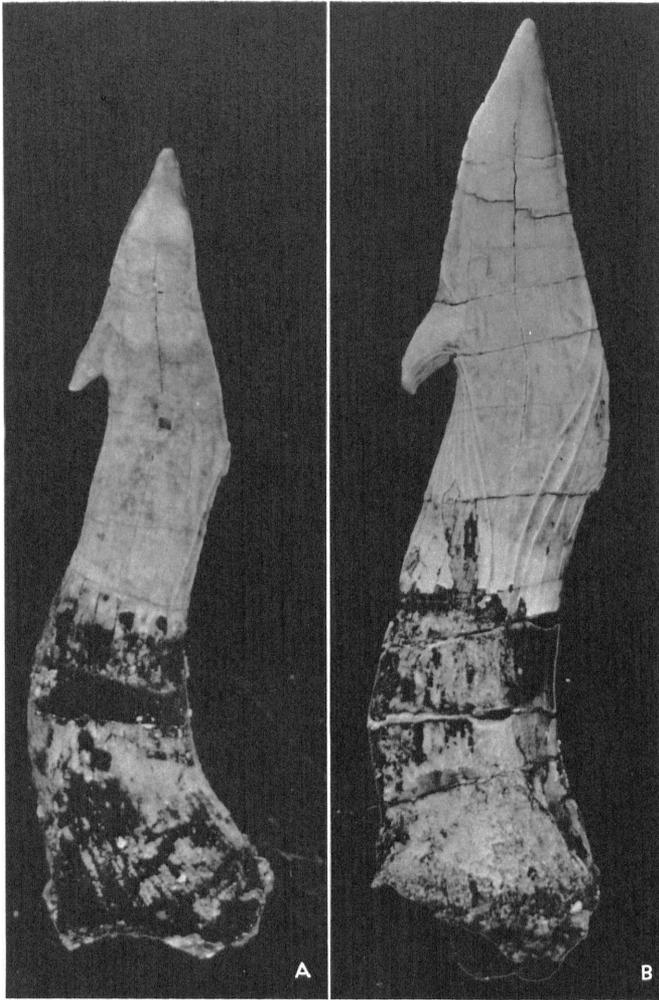
FIG. 2. *Pucapristis branisi*, rostral teeth. A. A.M.N.H. No. 8680. B. A.M.N.H. No. 8678. Photographed in ultraviolet light, to show extent of enamel layer. × 3.

veloping tooth and induces the differentiation of the dentine-forming cells. Dentine, however, frequently develops beyond the limits of this layer in the elasmobranchs, but osteodentine probably does not form the entire tooth base. The bases of the dermal denticles and teeth in sharks may include osteodentine, but at least the zone of attachment at the proximal end is probably invariably bone.

FIG. 3. *Pucapristis branisi*, longitudinal section of rostral tooth, A.M.N.H. No. 8681. A. Crown, including small portion of bony base, ×4. B. Apex of crown, ×10. Owing to the thinness of the section, the vascular canals appear as short, vertical, occasionally anastomosing black lines.

There are marked differences in the microstructure of the rostral teeth in *Onchopristis* and *Onchosaurus*. In the former, the crown is composed of orthodentine, and, in the latter, of osteodentine in the form of vertical dentinal osteons. The base in both genera probably consists of convoluted osteodentine and bone. The close resemblance in the crown histology of the *Onchosaurus* and *Pucapristis* rostral teeth suggests that these genera are more closely related to each other than either is to *Onchopristis*. The absence of dentine in the base of the *Pucapristis* teeth may be a peculiarity of this genus.
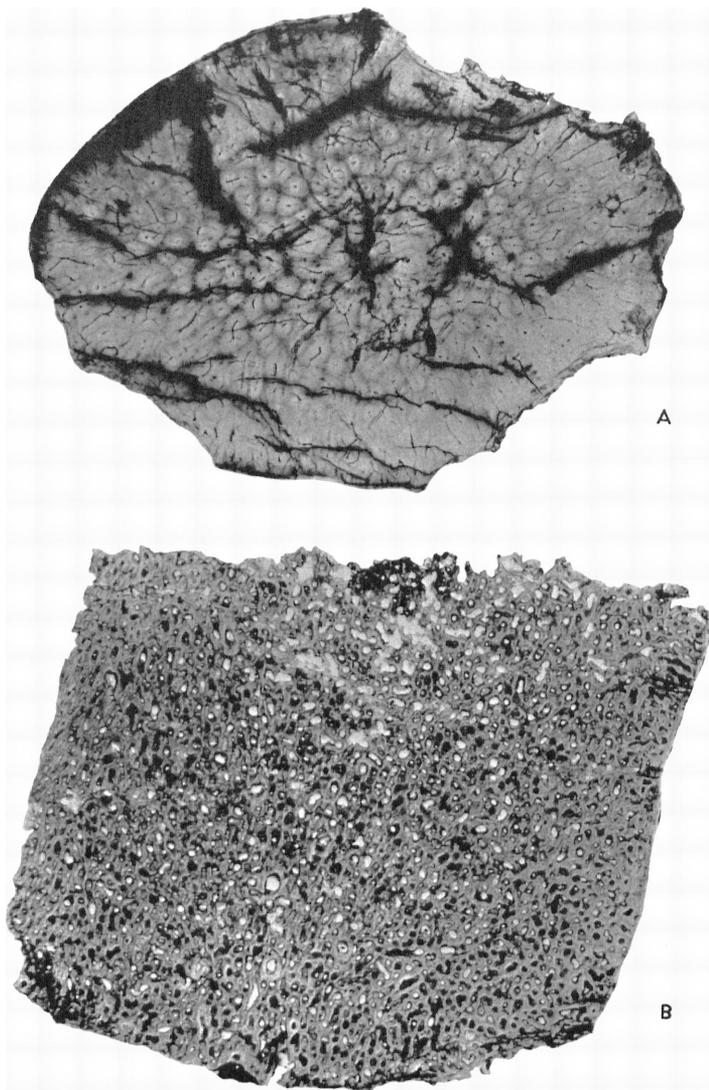
FIG. 4. *Pucapristis branisi*. A. Transverse section through crown of rostral tooth at level of ribbed enamel. Note typical dentinal osteons. The enamel is present on the upper left surface. B. Transverse section through base. This tissue appears to be bone, with relatively large vascular canals. There is no evidence of dentine. Both × 10.

OTHER FISH REMAINS FROM THE
EL MOLINO FORMATION

The batoid remains from the El Molino bone bed at Torotoro include *Rhombodus*-like teeth plus teeth similar to those of *Dasyatis* and *Raja*. Because of inadequate comparative material, however, generic identification has not been attempted.

The *Rhombodus*-like teeth have high rhombic crowns, with slightly concave sides covered with fine vertical wrinkles. The unworn occlusal surface is flat and has five rounded, closely approximated, and gently curved diagonal ridges. Finer crenulations, more or less at right angles to the larger ones, cover the remaining surface. They are continuous with the side wrinkles. The root, which is set at a slight tilt to the crown, is relatively longer than that of *Rhombodus* (Arambourg, 1952, pl. 30). The bifurcation of the root begins some distance below the crown as in some *Myledaphus* teeth. There are no canal foramina between the bifurcated roots as in *Rhombodus* (Casier, 1947, fig. 7b) and *Myledaphus*. A single, large foramen, however, is situated on one side of the root immediately above the bifurcation.

Teeth identified as those of *Rhombodus* have been reported from the Senonian Quiriquina Formation of Chile (Schneider, 1936). The Upper Cretaceous portion of the Sergipe Series in Brazil has also produced teeth of this type (Löfgren and Oliveira, 1943, pl. 6). Unfortunately the description and figures are inadequate for proper comparison with the Torotoro specimens.

Tooth form in the dasyatid complex is highly variable, and there is a complete morphologic intergradation from *Rhombodus* and *Dasyatis* at one end to *Myledaphus* and *Parapalaeobates* at the other (R. Estes, personal communication). In view of this fact, a realistic generic allocation of the El Molino specimens is not currently possible. The crown and the root characters suggest, however, that a new taxon may eventually be required.

The *Dasyatis*-like teeth from Torotoro have smooth, rounded crowns, and resemble the teeth assigned to this genus by Arambourg (1952, pl. 31). The crowns of another type, also from Torotoro, have a spine and a sharp, W-shaped crest that suggest the Rajidae. Arambourg (*ibid.*, p. 178) has noted the close resemblance between rajid and dasyatid teeth. Isolated specimens are very difficult to identify with any degree of certainty.

The clupeid fish from the El Molino at Cayara is similar in body form to *Diplomystus longicostatus* Cope from the Upper Cretaceous Ilhas Forma-
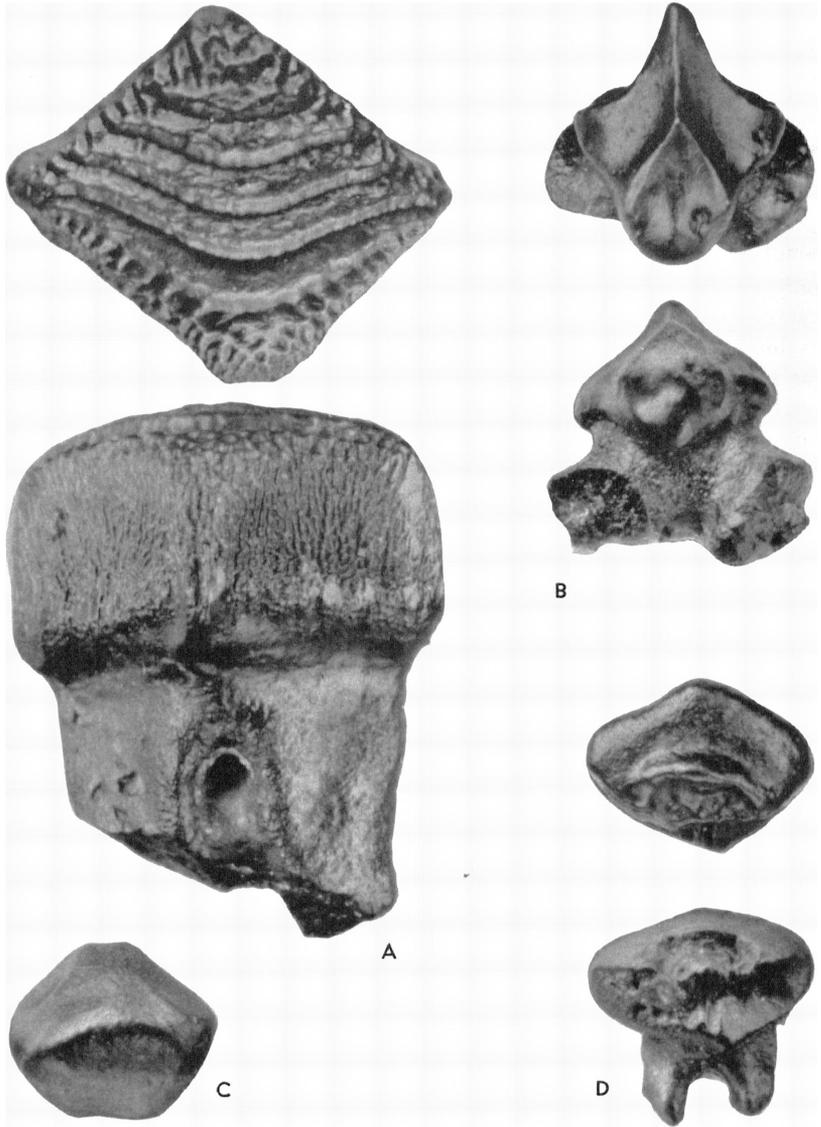
FIG. 5. Batoid teeth from the El Molino Formation. A. *Rhombodus*-like tooth in crown and side views, A.M.N.H. No. 8675. B. *Rajid*-like tooth in crown and side views, A.M.N.H. No. 8677. C. *Dasyatis*-like tooth in crown view, A.M.N.H. No. 8676. D. *Dasyatis*-like tooth in crown and lateral view, A.M.N.H. No. 8676. A, ×19; B–D, ×20.
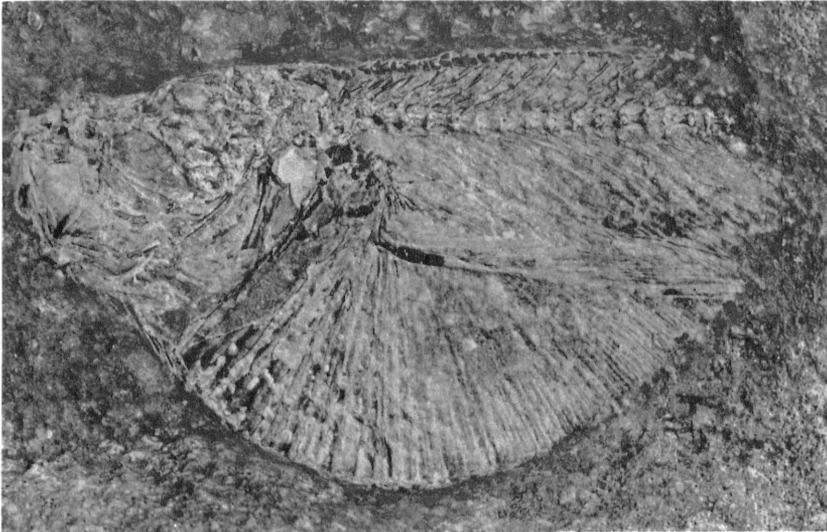
FIG. 6. Clupeid from the El Molino Formation, A.M.N.H. No. 8674, one of several incomplete specimens showing dorsal scutes, convergence of ventral scutes, and elongated pectoral fin. ×3.5.

tion of the Bahia Series in Brazil (Schaeffer, 1947). Although the available specimens are fragmentary, it is evident that the body is relatively short and deep. The dorsal scutes are winged as in *D. longicostatus*, but the pectoral fins have a higher insertion, are much longer, and give the fish a rather *Gasteropelecus*-like appearance. Another unusual feature is the apparent convergence of the ventral scutes toward a point not far behind the shoulder girdle and below the second or third vertebra. This convergence, which has been observed in four specimens, does not occur in other deep-bodied clupeids such as *D. birdi* from Mt. Lebanon. The Cayara form must represent at least a new genus. It will be described on the basis of complete specimens by Mlle. Y. Signeux of the Institut de Paléontologie, Paris.

The fauna of the El Molino, as listed by Lohmann and Braniša (1962), includes both marine and brackish- to fresh-water invertebrates. The turtle fragments from Vila Vila are probably pleurodire (Georg Zappler, personal communication) and therefore represent a fresh-water type. Dinosaur tracks have also been discovered. The fishes from the bone bed at Torotoro could be marine, brackish-, or possibly, but less probably, fresh-water forms. This evidence indicates a marginal marine environ-

ment with periodic withdrawals of the sea from the southern end of the basin in the Central Cordilleras of Peru and Bolivia, as indicated by Harrington (1962, fig. 25). Since this basin disappeared by the Turonian (*ibid.*, fig. 26), and the ganopristines are unknown earlier than the Cenomanian, a Cenomanian age for the El Molino is indicated.

COMMENTS ON PRISTID EVOLUTION

Arambourg (1935) has proposed two subfamilies within the Pristidae on the basis of the structure and attachment of the rostral teeth. The Ganopristinae, to which *Pucapristis* is assigned, have rostral teeth with a compressed, enamel-covered crown and an expanded base attached to the rostrum by connective tissue. In the Pristinae, enamel is present only at the apex of recently erupted teeth, and there is no expanded basal portion. The teeth are fixed in sockets along the edges of the rostrum.

Although the pristids are galeoid-like in general body form, a rhino-batid ancestry is indicated by numerous internal characters (Jaekel, 1894; Hoffmann, 1913; Holmgren, 1941). The primary adaptive significance of the free, elongated rostrum (moderately elongated in the rhino-batoids to support the anterior extensions of the pectoral fins) and of the shark-like body form may be related to mud grubbing and the maneuverability required for this activity. Enlargement of the dermal denticles along the edge of the rostrum to form the rostral teeth may well represent a secondary adaptation for slashing prey.

The ganopristines are known from the Cenomanian to the Danian, and the pristines from the Yprésien to the Recent. Casier (1954) has questioned the desirability of retaining both groups in one family. Although the exact relationship between them is unknown, it is probable that some ganopristine stock gave rise to the pristines. Except for certain differences in tooth histology and mode of tooth attachment, the skeleton of the ganopristines is apparently identical with that of the pristines. Since the rostral teeth represent modified denticles, attachment to the rostrum by connective tissue must have preceded implantation in sockets.

If gaps in the fossil record are allowed for, it is probable that the gano-pristines were replaced by the pristines at the beginning of the Tertiary. This replacement may well be related to the mode of tooth attachment. Rostral teeth embedded into sockets could provide a more rigid slashing organ and be more resistant to detachment during grubbing than the ganopristine type.

The various shapes of the rostral teeth in the ganopristines (Arambourg, 1940) perhaps reflect differences in prey preferences or in slashing

behavior. Grubbing with the rostrum probably had a minimal influence on the shape of the rostral teeth, unless they were greatly elongated. In *Ctenopristis* (Arambourg, 1940, 1952) the long, delicate, awl-shaped rostral teeth were directed posteriorly, presumably making them less vulnerable during bottom feeding. The obvious correlation between variable versus constant tooth form and mode of attachment suggests that selection for tooth implantation and continuous tooth growth in the pristines also involved selection for straight, peg-like teeth.

The relationships of the various ganopristine genera considered by Arambourg (1940) are difficult to determine. On the basis of rostral tooth microstructure, however, they can be divided into two groups represented by *Onchopristis* and *Onchosaurus*. In *Onchopristis*, as noted above, the crown is composed of orthodentine covered with a thin layer of enamel. The crown of *O. dunklei* from the Woodbine Formation of Texas has a fairly extensive pulp cavity (McNulty and Slaughter, 1962), but in *O. numidus* (Stromer, 1917, pl. 1, fig. 12) the cavity is reduced to a narrow vascular canal. The base consists of osteodentine and bone.

The crown and peduncle of the *Onchosaurus* tooth are composed of osteodentine, with vertical, anastomosing, dentinal osteons (Stromer, 1917, pl. 1, fig. 23). Although not indicated in Stromer's (1922, fig. 11) figure, the crown is presumably covered with pallial dentine and enamel. The base is made up of convoluted osteodentine and probably also of bone.

The rostral teeth of *Sclerorhynchus* (Cenomanian-Maestrichtian), *Ganopristis* (Cenomanian-Danian; considered to be a synonym of *Sclerorhynchus* by Arambourg, 1952, p. 188), and *Ctenopristis* (Maestrichtian) have a microstructure similar to that of *Onchopristis* (Arambourg, 1940). *Marckgrafia* (Cenomanian; Weiler, 1935) probably also belongs to the *Onchopristis* group, as well as *Dalpiazia* (Maestrichtian) and *Ischyrhiza* (regarded as a subgenus of *Onchosaurus* by Arambourg, 1940, but see Wetzel, 1930, p. 96). *Schizorhiza* (Senonian-Danian) has an osteodentine crown (Weiler, 1930, pl. 4, figs. 2, 4) as do *Pucapristis* and *Onchosaurus*.

The microstructure of elasmobranch placoid scales has not been investigated systematically, but it is known to be quite variable. The crown may be composed of either orthodentine or osteodentine, and the pulp cavity is variously developed. The basal plate is usually formed of bone (Ørvig, 1951, p. 361), although osteodentine may also be present in some forms. The two types of ganopristine teeth conceivably could have arisen from either sort of placoid denticle through suppression of intervascular bony trabecles in the pulp chamber, resulting in orthodentine, or by the development of trabecles to form osteodentine. The micro-

structure of the ancestral type is, of course, unknown, and no description of the histology of the rhinobatid dermal denticles is available.

The unerupted rostral tooth of *Pristis cuspidatus* (Engel, 1910) is similar to that of *Onchosaurus* (Stromer, 1922, fig. 11), except for the absence of a basal portion. The apex of the crown is covered with pallial dentine and enamel which tend to be worn away shortly after the tooth becomes functional. The crown thus resembles the *Onchosaurus* type, and it is reasonable to conclude that the pristines arose from an *Onchosaurus*-like ancestor. Elimination of the base in the pristines would permit the rostral teeth to grow by continuous lengthening of the vertical dentinal osteons.

TABLE 1
ADAPTIVE LEVELS IN PRISTID EVOLUTION

Pristine level	Rostral teeth composed of osteodentine, set in sockets, base absent. Growth of rostral teeth continuous. Rostrum used for grubbing and slashing. Tertiary-Recent
Ganopristine level	*Onchopristis* group: Rostral teeth composed of orthodentine, with base *Onchosaurus* group: Rostral teeth composed of osteodentine, with base Marginal denticles enlarged to form rostral teeth attached by connective tissue. Rostrum used for grubbing and slashing. Upper Cretaceous
Prepristid level	Unknown, but rostrum presumably longer, more compressed, used for grubbing. Pectoral fins reduced, body more galeoid-like. ?Lower Cretaceous
Rhinobatid level	Rostrum moderately elongated, supporting anterior extension of pectoral fin. Upper Jurassic

The similar structure of the calcified rostrum in the ganopristines and the pristines also indicates a ganopristine ancestry (Stromer, 1922).

Except for minor variations, all the teeth on a *Pristis* rostrum are of about the same length, which indicates more or less synchronous eruption. The absence of tooth replacement in the pristine rostrum is well known. If a rostral tooth of *Pristis* is torn away from its socket, the space is covered with scar tissue. The teeth of the *Onchopristis* rostrum differ markedly in size (Stromer, 1925, pl. 1, fig. 5), which suggests some sort of heterochronic eruption in the ganopristines. The evidence is not conclusive, however, and the method of rostral tooth enlargement or replacement in the ganopristines is still problematic.

Propristis from the Upper Eocene of Egypt must represent a divergent

specialization from some ganopristine stock. The short, wide, and compressed rostral teeth of this genus are apparently composed only of convoluted osteodentine and are not set in sockets (Stromer, 1922).

The history of the pristids can thus be divided into three successive adaptive levels or grades (excluding the rhinobatid one) on the basis of the rostral teeth. The first, which is not represented in the fossil record, was actually pre-pristid. It presumably involved a retreat of the pectoral fins from the rostrum, compression and further lengthening of the rostrum for grubbing, development of a more galeoid-like body form, and perhaps the beginning of placoid scale enlargement along the edges of the rostrum. Since the rhinobatid rostrum is used to some extent for grubbing, it may be regarded as preadapted for its ganopristine function. Compression and further elongation simply improved its efficiency.

The next level, exemplified by the ganopristines, was attained by further enlargement of the marginal denticles to form rostral teeth. Since the structure of the ancestral denticles is unknown, it is not possible to determine whether the *Onchopristis* or the *Onchosaurus* type is more primitive. Both were present in the Cenomanian when the pristids appeared in the fossil record. They are regarded here as components of the same broad adaptive level.

The third level, represented by *Pristis*, probably arose from the *Onchosaurus* group with the disappearance of the basal portion of the rostral teeth, the development of a mechanism for continuous growth of the vertical dentinal osteons, and the implantation of the teeth in alveoli. Within the limitations imposed by their ganopristine ancestry, the pristines evolved a new and presumably more effective method of equating tooth size with rostral growth, and perhaps functionally related, the development of a firmer type of tooth attachment.

The occurrence of either osteodentine or orthodentine as the principal component of the ganopristine rostral teeth represents an interesting problem in the evolution and morphogenesis of the dental tissues. A comparable situation is found in the galeoid sharks. The teeth of the "lamid group" have osteodentine crowns and those of the carcharinids (*sensu lato*) have orthodentine crowns (Beaumont, 1959). Both are derived from an unknown hybodont stock. The crowns of *Hybodus* teeth are composed of osteodentine, as are also those of *Cladodus* (Gross, 1938) which is at least a structural ancestor of *Hybodus*. In all these forms, the crown is covered with a layer of pallial dentine and enamel.

Ørvig (1951, pp. 392–393, 435–436) implies that a crown composed of osteodentine covered with pallial dentine represents the primitive condition. If so, the change from osteodentine to orthodentine must have

occurred several times independently in the elasmobranchs. This question has also been discussed by Marquard (1946), but no conclusion is reached. The fact that pallial dentine usually develops ontogenetically before the orthodentine does not alter the phylogenetic picture.

Ørvig (*ibid.*, p. 393) notes that the large jaw teeth of the holosteans *Sargodon* and *Colobodus* (*Nephrotus*) are composed of osteodentine covered with pallial dentine, but the smaller teeth are made up of orthodentine. The teeth of the holostean *Hypsocormus* (*ibid.*, p. 345) show the same pattern, but those of intermediate size consist only of bony trabecles covered with pallial dentine. In *Colobodus* the large teeth have probable vestiges of intervascular bony trabecles in the pulp cavity. Although these observations indicate that a change from osteodentine to orthodentine has occurred by reduction of the trabecles and subsequent elaboration only of the dentine, they do not explain why such a shift in the microstructure should occur. The possibility that both tissues may occur in the same dentition indicates that caution is necessary in using them as taxonomic characters. All the teeth in a single elasmobranch dentition, however, apparently have the same basic microstructure, regardless of the degree of heterodonty.

The adaptive significance, if any, of this shift in crown histology is obscure. There is as yet no convincing evidence that a crown composed of osteodentine is stronger or more resistant to wear than one composed of orthodentine, or vice versa. The teeth of many fishes that grind or crush their food are made up of osteodentine with vertical dentinal osteons (Radinsky, 1961). On the other hand, numerous fishes besides the carcharinid sharks and the *Onchopristis*-like ganopristines have tooth crowns composed of orthodentine, including some that grind their food (e.g., most of the teleosts).

It is not possible to conclude from the above evidence that osteodentine in the form of vertical dentinal osteons is a more resistant tissue than orthodentine, although it must be admitted that Radinsky's evidence points in this direction. But, if true, why has there been a frequent shift to orthodentine? Perhaps an answer will be found when the morphogenetic mechanisms involved are more completely understood.

The frequently noted convergence of the Pristiophoridae with the Pristidae involves another interesting facet of pristid evolution, particularly since representatives of both families have had overlapping distributions, possibly throughout their history. Although they are clearly unrelated, as indicated by numerous internal and external characters, the superficial resemblance is rather striking, and a similar way of life is evident.

The feeding behavior of *Pristiophorus* is poorly known, but it is probable that the rostrum is used for grubbing and slashing. The rostral teeth are made up of orthodentine with a reduced base of the same tissue. The tentacles situated midway on the rostrum apparently function as taste organs (Hoffmann, 1913). The Cretaceous *Propistiophorus* does not have enlarged denticles along the margin of the rostrum (Woodward, 1932). Initial development of this structure in relation to grubbing is therefore a distinct possibility.

The pristiophorids, like the pristids, appeared in the Late Cretaceous, and both families are represented in the Mt. Lebanon fauna (*Sclerorhynchus* and *Propristiophorus*). Remains of *Pristis* and *Pristiophorus* have been found in the Miocene of Europe (Casier, 1954). The geographical ranges of at least one species in each family overlap along the coasts of southern Africa (Smith, 1953), western Australia (Whitley, 1940), and perhaps elsewhere in the Indo-Pacific region.

Although the ecological niches occupied by the pristids and the pristiophorids have undoubtedly shared many factors in common throughout their history, there is evidence that competition between them has always been minimal or non-existent in spite of some range overlap. *Pristis* is a shallow-water, coastal, estuarine, and occasionally fresh-water form. The ganopristines and the Tertiary pristines probably inhabited similar environments, as suggested by the relative abundance of rostral teeth in coastal and epicontinental sea sediments. Modern pristiophorids inhabit deeper water, from about 10 to 200 fathoms. The Upper Cretaceous Mt. Lebanon assemblage is a mixture of shallow-water or pelagic and deep-ranging types. *Propristiophorus* could very well represent a relatively deep-water form and *Sclerorhynchus* a shallow-water one.

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