

Schizorhiza: a unique sawfish paradigm from the Difunta Group, Coahuila, Mexico

James I. Kirkland^{1*} and Martha Carolina Aguilón-Martínez²

¹Utah Geological Survey, P.O. Box 146100, Salt Lake City, UT 84114-6100, U.S.A.

²SEPC-Museo del Desierto, Prol. Pérez Treviño 3745, Centro,
25015 Saltillo, Coahuila, México.

* e-mail: jkirklan.nrugs@state.ut.us

ABSTRACT

The sclerorhynchid sawfish *Schizorhiza* is widespread in Upper Cretaceous marine strata of the Difunta Group of Coahuila, Mexico ranging from the latest Campanian to latest Maastrichtian. A fragmentary rostrum from the latest Campanian Cerro de Pueblo Formation provides significant new information about this sawfish.

The rostrum of *Schizorhiza* is similar to that of other known Sclerorhynchidae species in its gradual taper and in that superficial ophthalmic nerves run down the dorsal grooves and the bucco-pharyngeal nerves run down the ventral grooves. Unlike other sclerorhynchids, it was discovered that the distinctive diamond shaped rostral teeth with their flaring roots were not shed with the addition of alternating replacement teeth. This results in *Schizorhiza* small teeth being densely packed into files to produce a continuous, sharp, serrated edge down each side of a rostrum that is more than 50 cm in length. This rostral tooth pattern is unique among the Sclerorhynchoidea and indicates that rather than probing for food in soft sediments with a comb-like rostrum as other sawfish, *Schizorhiza* specialized in hunting fish with its truly saw-like rostrum.

Keywords: *Schizorhiza*, sawfish, Difunta Group, Coahuila, Mexico.

RESUMEN

El descubrimiento de un rostro fragmentado asignado al pez sierra *Schizorhiza* en la formación Cerro del Pueblo del Campaniano tardío, proporciona información nueva y significativa para este grupo de peces de la Familia Sclerorhynchidae. Este grupo se encuentra ampliamente distribuido en los estratos marinos del Cretácico Superior del Grupo Difunta en Coahuila, México, en un rango que va del Campaniano tardío al Maestrichtiano tardío.

El rostro de *Schizorhiza* es similar a aquellos de las otras especies conocidas de peces esclerorrincoideos, en su adelgazamiento gradual y en que los nervios superficiales oftálmicos corren abajo de los surcos dorsales y los nervios bucofaringeos corren abajo de los surcos ventrales. La mayor importancia de este hallazgo fue descubrir que la forma distintiva de diamante de los dientes rostrales, con sus raíces ensanchadas, no eran mudables, pero podían ser reemplazados. Esto da como resultado que los pequeños dientes de *Schizorhiza* estuvieran densamente empaquetados en filas, produciendo un borde aserrado y agudo abajo de cada lado del rostro que tenía una longitud aproximada de 50 cm. Este patrón de dientes rostrales es único entre los esclerorrincoideos e indica que los peces más que "sondear" por comida en sedimentos suaves, con un rostro parecido a un peine como otros peces sierra, *Schizorhiza* se especializaba en cazar peces con un rostro verdaderamente parecido a una sierra.

Palabras clave: *Schizorhiza*, pez sierra, Grupo Difunta, Coahuila, México.

INTRODUCTION

The Difunta Group consists of approximately 4,000 m of intertonguing terrestrial and marine strata spanning the uppermost Campanian to lower Eocene without any recognized stratigraphic breaks and has been subdivided into seven formations (Figure 1) in the central Parras basin west of Saltillo, Mexico (Murray *et al.*, 1962; Weidie and Murray, 1967; Weidie *et al.*, 1972; McBride *et al.*, 1974).

The paleontology of the Late Cretaceous Difunta Group in Coahuila, Mexico, is poorly know. At present, there have been descriptive papers of some of the invertebrate taxa (Imlay, 1937; Wolleben, 1977) and research on the vertebrate fauna is underway (Hernández, 1992; Hernández and Kirkland, 1992; Rodríguez-de la Rosa and Cevallos-Ferriz, 1998; Kirkland *et al.*, 2000). The discovery of an isolated tooth of *Schizorhiza* in the basal Rancho Nuevo Formation supports placement of the Cretaceous-Tertiary boundary above the base of the Rancho Nuevo Formation. The recent discovery of a rostrum of the sclerorhynchid sawfish *Schizorhiza* by the junior author reveals features unrecognized in any other sawfish rostrum and supports the placement of *Schizorhiza* in a distinct subfamily of sclerorhynchid sawfish.

THE RANCHO NUEVO ROSTRAL TOOTH

The first specimen of the *Schizorhiza* (SEPCPV-15/302) recognized in Coahuila, Mexico, was discovered in 1993 by Carlos René Delgado de Jesús of the Coahuila Paleontological Commission at Canyon El Barril

north of Saltillo, Coahuila, Mexico (SEPCP loc. 15). It was recovered in an isolated sandstone block from the basal calcareous sandstone unit of the Rancho Nuevo Formation (Figure 1). Other elasmobranch material from this unit includes *Serratolamna serrata* (Agassiz), *Scapanorhynchus texanus* (Roemer), and *Pseudocorax* sp.

The rostral tooth is embedded in matrix such that only one dorsoventrally flattened side is visible (Figure 2). It is 14.0 mm tall with an enamelloid cap 4.1 mm tall and 4.9 mm wide. The slightly asymmetrical cap is roughly arrow shaped with sharp cutting edges. The base of the cap is strongly constricted at its contact with the peduncle, which expands sharply toward its base. The base is subdivided by 3 deep indentations corresponding to grooves on the face of the peduncle, such that four long prongs are developed on the basal portion of the peduncle. The medial two prongs at 4.3 mm are the longest.

This unit had been identified as basal Paleocene by previous researchers (Murray *et al.*, 1959, 1962; Wolleben, 1977; Kauffman, personal communication).

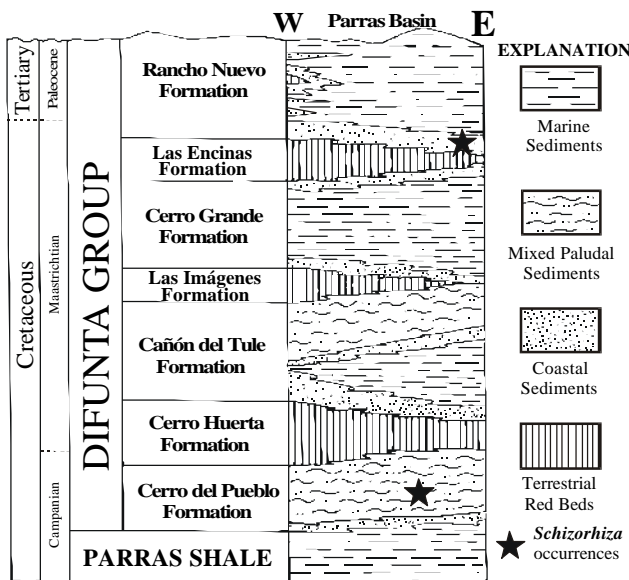


Figure 1. Difunta Group as developed in the central Parras Basin near Saltillo, Coahuila, Mexico with stratigraphic horizons bearing *Schizorhiza* specimens indicated. Modified after Kirkland *et al.* (2000).



Figure 2. *Schizorhiza* tooth (SEPCPV-15/302) from basal Rancho Nuevo Formation.

Sclerorhynchid sawfish are not recognized above the Cretaceous/Tertiary boundary (Cappetta, 1987b, 1990). It was thought that this might represent either an example of a Sclerorhynchid sawfish in the basal Tertiary or as in a number of other examples (Cappetta, 1987b; Eaton *et al.*, 1989) reworking of Cretaceous elasmobranch material into Tertiary strata. The recent discovery of ammonite material stratigraphically higher in the Rancho Nuevo Formation requires that the Cretaceous - Tertiary boundary be placed somewhere within the lower Rancho Nuevo and that there is overlap of typical basal Paleocene and uppermost Cretaceous invertebrate taxa at this site (Kirkland *et al.*, 2000). Certainly this is an area, where further research on the Cretaceous/Tertiary boundary is warranted.

THE CERRO DEL PUEBLO ROSTRUM

In 1994, the junior author recovered a largely intact *Schizorhiza* rostrum (SEPCPV-1/303) preserved at the center of a weathered and fragmentary siderite concretion. Weak development of desert varnish indicates that the specimen had been exposed on the surface for many years. Parts of the original specimen were lost to erosion. The specimen had weathered out of an interval of marine shale 120 meters above the base of the Cerro del Pueblo Formation (SEPCPV loc. 1).

The rostrum was associated with a diverse invertebrate fauna including *Ethmocardium* sp., *Inoceramus vanuxemi* Meek and Hayden, *Cymprimera* sp., *Turritella vertibroides* Morton, *Eutrephoceras* sp., and *Sphenodiscus* sp. indicating shallow open marine conditions (Figure 3). Associated vertebrate remains include *Serratolamna serrata* (Agassiz), and dinosaur bones. The co-occurrence of *Inoceramus vanuxemi* and *Sphenodiscus* indicate a latest Campanian age for the strata correlative to the Nacatoch Sand of the Navarro Group in Texas (Stephenson, 1941) and the *Baculites reesidei* and *B. jenseni* ammonite zones in the Western Interior, USA (Kennedy *et al.*, 1992).

The concretion preserving the rostrum had been fractured in a somewhat regular pattern. There were numerous fractures crossing the rostrum at a high angle (Figure 4). The upper and lower halves of the concretion were split apart with the bulk of the rostrum remaining attached to the thicker side of the concretion. A few sections of the larger medial section of the rostrum were preserved separately. The rostrum was largely exposed along fractures along the outer surface of the prismatic calcified cartilage. Likewise the rostrum was fractured longitudinally into three sections along the line of the dorsal and ventral grooves, with the teeth being preserved in an additional section from along each side of the rostrum. The tooth rows were split along the divergent division of the peduncle into an upper and lower section. Although it is estimated that less than 50 % of the rostrum was found, the fragmentary condition of the

specimen reveal a number of anatomical details that might not have been observed otherwise.

The length of the preserved rostrum is 53 cm with the entire length of the rostrum estimated to be appreciably longer (Figure 4). It has a gradual taper of 5-6 degrees (Figure 5). The distal end is approximately 1 cm thick and is 3.8 cm wide with the rostral tooth rows extending out an additional 1.8 cm laterally on each side (total of 7.4 cm wide). The distal end appears to have been squared off, with the tooth rows diminishing rapidly in size as they bend around the end of the rostrum. The proximal end of the preserved rostrum is a maximum of 1.8 cm thick and is estimated at 8.2 cm wide with an estimated width of each tooth row of 2.2 cm (total of 12.6 cm wide). The splitting of the rostral cartilage at the proximal end within the matrix indicates the rostrum was separated from the rest of the fish prior to burial.

Two prominent grooves run down the top and bottom of the rostrum (Figure 5). The superficial ophthalmic nerves ran down the dorsal pair and the buccopharyngeal nerves ran down the ventral pair (Cappetta, 1980, 1987a). Both pairs of grooves expand from 6-13 mm wide posteriorly and are expand from 6-9 mm from the margins of the rostrum posteriorly. While flattened overall, the center of the rostrum is thickest between the grooves. The lateral margins of the rostrum below the rostral teeth are squared off along the entire length of the rostrum.

The surface of the rostrum is ornamented by fine longitudinal grooves averaging 25-30 per cm. Along the raised middle portion of the rostrum these fine grooves are superimposed over longitudinal ridges that average 6-8 per cm near the proximal end of the preserved rostrum. This ornamentation of the calcified rostral cartilage appears to be symmetrical between the upper and lower surfaces.

The largest preserved teeth have a total height of 12 mm. The enameloid tooth crown or cap is less than half the height of the complete tooth. The nearly symmetrical cap is flattened and triangular with sharp cutting edges. In dorsoventral view, there is a strong constriction of the basal cap and upper peduncle with a well-marked convex margin between the enameloid and the peduncle. In lateral view, the cap joins the peduncle smoothly as it divides into two strongly divergent lobes. In dorsoventral view, each lobe broadens toward the base, which is divided by three long indentations corresponding to grooves on each face. Whereas the rostral teeth are nearly symmetrical in dorsoventral view, the teeth are nearly perfectly symmetrical in lateral view. There is no noticeable difference in tooth form along the entire rostrum. The teeth 3.6 cm from the distal end of the rostrum have enameloid tooth crowns 4.0 mm wide and 3.1 mm tall. Tooth crowns 30 cm from the distal end of the rostrum are 5.3 mm wide and 4.1 mm tall. Thus, there is only a slight increase in tooth size from the distal to more proximal end of the rostrum.

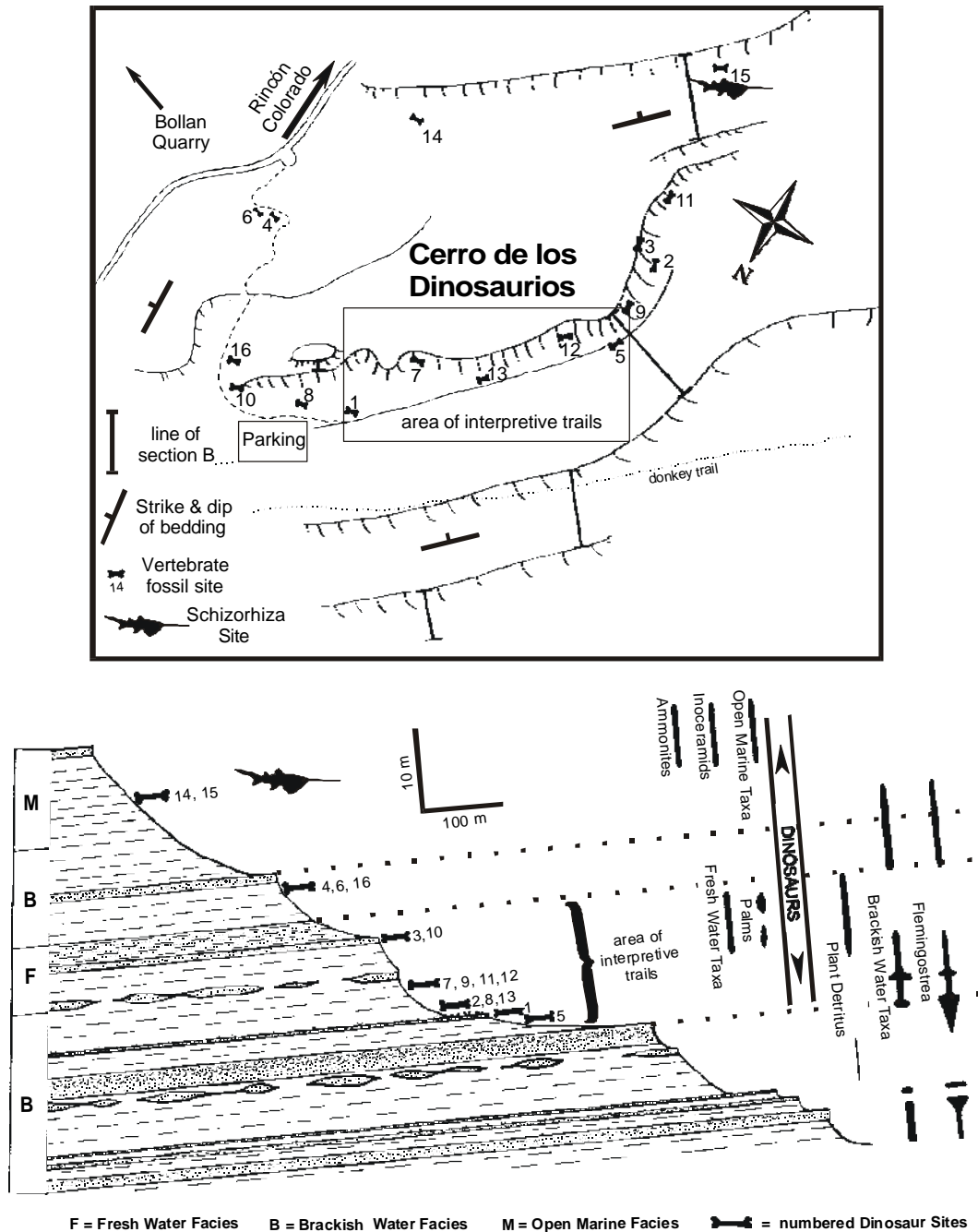


Figure 3. A) 1993 sketch map showing vertebrate localities around Cerro de los Dinosaurios and line of measured stratigraphic section. Location of recent improvements shown in boxes. Note position of north arrow. Strata dips south-southeast to southeast with resistant sandstone units holding up low ridges. Note location of *Schizorhiza* rostrum locality SEPCPV 1. No scale intended. B) Stratigraphic section of a portion of the Cerro del Pueblo Formation at Cerro de los Dinosaurios showing distribution of vertebrate sites, major faunal groups, and the resulting interpretation of salinity changes through the section. Modified after Kirkland *et al.* (2000).

The teeth are arranged in a very tight pattern forming a dental battery (Figure 6). Each exposed tooth is closely underlain by a replacement tooth that resides between the flaring lobes of the peduncle. Three teeth underlie each exposed tooth crown in this way forming files. As the rostral teeth are slightly asymmetrical in

dorsoventral view, each successive tooth crown is displaced slightly away from the apex of the rostrum. Each tooth file is closely appressed to its adjoining tooth files, with the tooth caps alternating such that adjoining tooth caps are positioned between the teeth in the constrictions between tooth caps and peduncles. It is estimated that

there are between 110 and 120 tooth files down each side of the rostrum with more than 1,800 rostral teeth in position at any time. The rostral tooth battery abuts closely with, but does not touch the calcified cartilage along the flattened lateral margin of the rostrum (Figure 5).

SAWFISH ROSTRUMS

Schaeffer (1963) has discussed the development of the sawfish rostrum from a bottom dwelling rhinobatoid ancestor by the elongation of the rostrum and the development of rostral teeth from placoid scales. The rostrum was used for both grubbing in the mud for invertebrates and for slashing through the water at swimming prey such as fish and squids. Following previous researchers, he distinguished a primitive group; ganopris-

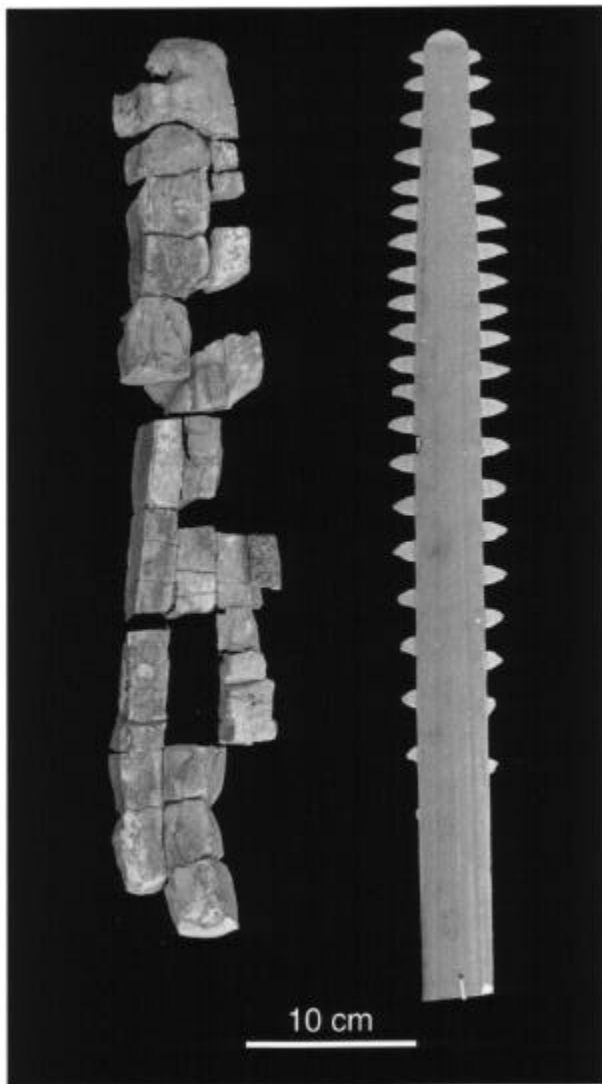


Figure 4. *Schizorhiza* rostrum (SEPCPV-1/303) as recovered compared to similar sized rostrum of the modern sawfish, *Anoxypristis*.

tids (=Sclerorhynchidae), where the rostral teeth were attached by connective tissue, and the modern group; pristids, where the rostral teeth were set in sockets. In both groups, the teeth were largely elongate and extend laterally to form a comb-like structure. This structure was capable of both pulling invertebrates out of the sediment and injuring fish.

Cappetta (1974) demonstrated on anatomical grounds that the Sclerorhynchoidea and Pristoidea were independently derived from the Rhinobatoidea. The pristids do not appear until the lower Eocene, well after the sclerorhynchids go extinct (Cappetta, 1987a, 1987b). Thus the Sclerorhynchoidea, the Pristoidea, and the sawsharks Pristiophoroidea are all convergent on the same body plan for grubbing and slashing for prey. Cappetta (1987b) also demonstrated that the Sclerorhynchoidea and Pristiophoroidea convergent in the form of their rostrums in that they both tapered and bore the superficial ophthalmic nerves in dorsal grooves and the buccopharyngeal nerves in ventral grooves on the rostrum (Figure 7). This is probably a primitive developmental similarity. The Pristoidea differ in having rostra with parallel sides (Figure 8) and in having these nerves enclosed within the rostrum (Figure 7).

Modern pristids do not replace their teeth, as they continuously grow from sockets. However, both the sawsharks and the sclerorhynchids appear to have replaced their teeth throughout their lives (Slaughter and Springer, 1968). In *Sclerorhynchus atavis* Woodward, the development of new rostral teeth begins by the formation of an elongate enameloid crown in a horizontal orientation

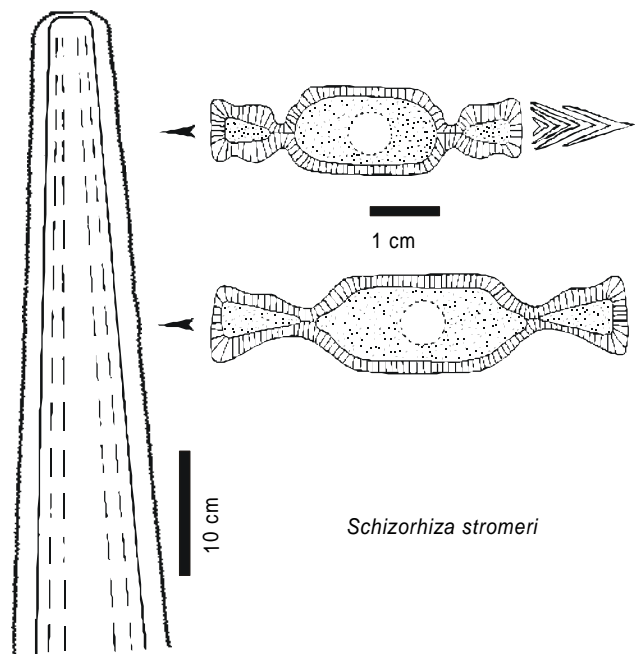


Figure 5. Reconstruction of *Schizorhiza* rostrum in dorsal view and in cross-section.

within the tissue between the bases of previously erupted teeth. As the peduncle begins to develop, it erupts by slowly rotating into an erect orientation (Figure 9). This results in an irregular spacing of large and small teeth along the rostrum.

The development of a rostral tooth battery in *Schizorhiza* demonstrates a regularity in tooth replacement unknown and unsuspected in any sclerorhynchid genus. The result is to produce a sharp serrated enameloid edge on the rostrum that is always maintained. As this edge has little relief, it would not be very practical for grubbing in the mud for invertebrates, but it would be very effective at slashing at fish. Thus, it appears that *Schizorhiza* was specialized for attacking prey in open water more in line with behaviors documented for modern billfish.

Cappetta (1991) has recognized oral teeth that he has assigned to *Schizorhiza*. These teeth are more high crowned than in most sclerorhynchids, but are very small and would have been of little use in any capacity beyond manipulating its prey (Figure 10).

Sclerorhynchus has a long whip-like tail (Figure 11a) inefficient for propulsion in open water and was probably a bottom dweller. *Pristis* and *Anoxypristis* have significantly deeper tails than does *Sclerorhynchus* and are known to feed on fishes in addition to benthic feeding. With the obvious adaptations of *Schizorhiza* for slashing in open water, a more lunate tail like that of *Pristis* is predicted (Figure 11b).

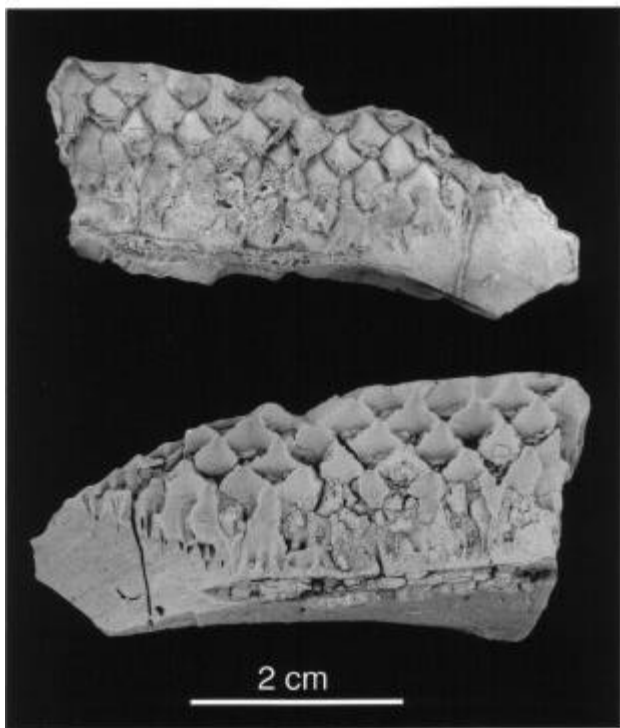


Figure 6. Fragments of the rostral tooth battery of *Schizorhiza* (SEPCPV-1/303) split along center.

SYSTEMATIC PALAEOONTOLOGY

Repository. SEPCPV Coordinación de Paleontología, S.E.P.C.- Museo del Desierto. Paleontological Collection-Vertebrates. Saltillo, Coahuila, México.

Suborder Sclerorhynchoidea
Family Sclerorhynchidae
Subfamily Schizorhizinae New Subfam.

Diagnosis. Sclerorhynchoid sawfish with rostral teeth forming a dental battery of overlapping teeth, such that a continuous enameloid edge is present along each side of the rostrum even as rostral teeth are shed.

Genus *Schizorhiza* Weiler, 1930

Type Species. *Schizorhiza stromeri* Weiler, 1930.

Diagnosis. Oral teeth very small (1.6-2.5 mm tall, 1-2 mm wide), with tall recurved central cusp bearing lateral

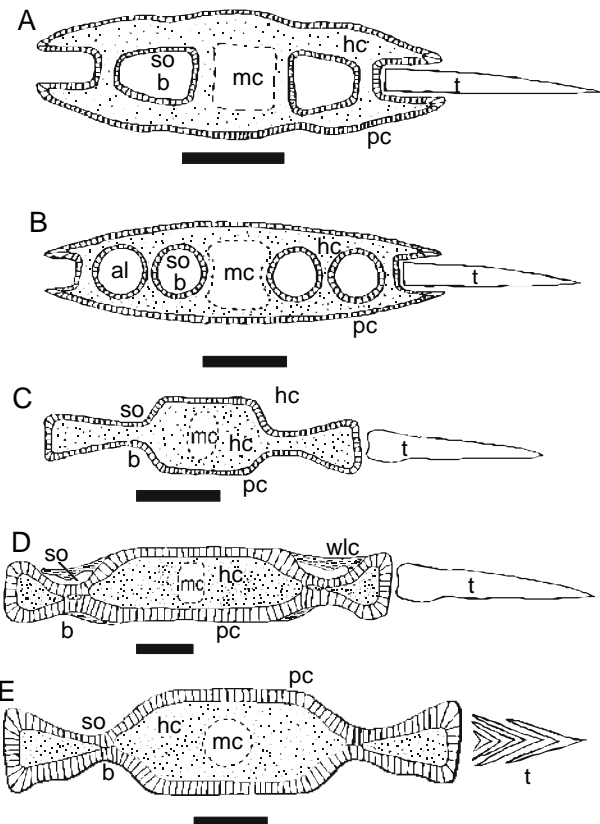


Figure 7. Cross-sections of sawfish and sawshark rostrums. A) the modern sawfish, *Pristis pristis*; B) the modern sawfish *Anoxypristis cuspidatus*; C) the sawshark *Pristophorus nudipinnis*; D) the sclerorhynchid sawfish *Onchopristis numidus*; E) the sclerorhynchid sawfish *Schizorhiza stromeri*. Abbreviations: al = position of nerves for ampullae of Lorenzini; b = position of buccopharyngeal nerves; hc = hyalin cartilage; mc = medial canal; pc = prismatic calcite; so = position of superficial ophthalmic nerves; t = teeth; wlc = wood-like cartilage.

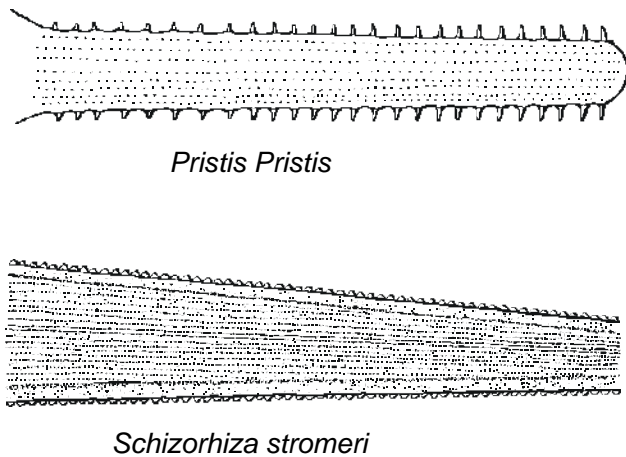


Figure 8. Comparison of the rostrum shape in *Schizorhiza* and *Pristis*.

carinae that rise into very weak lateral cusps. Rostral teeth small (10-20 mm tall, 4-8 mm wide); flat, triangular- to diamond-shaped cap with sharp cutting edges, much shorter than peduncle; a strong constriction is present below the cap from which the long peduncle divides into two strongly divergent lobes; each lobe expands toward its base which splits into four extensions derived from folds on the basal surface of each face; new teeth form within space of divided peduncle with four to five teeth in each tooth file at one time; tooth files adjoining and alternating.

Schizorhiza stromeri Weiler, 1930

- 1930 *Schizorhiza stromeri* Weiler, p. 20-23, pl. 2, figs. 1-8, pl. 4, figs. 2-4.
 1933 *Schizorhiza weileri* Serra, p. 103-108, figs. 1-7.
 1948 *Schizorhiza* cf. *weileri* Serra; Dunkle, p. 174-175, fig. 2.
 1952 *Schizorhiza stromeri* Weiler; Arambourg, p. 193-194, pl. 29, figs. 12-20.
 1987a *Schizorhiza stromeri* Weiler; Cappetta, p. 155, fig. 133.
 1991 *Schizorhiza stromeri* Weiler; Cappetta, p. 24-25, pl. 5, figs. 1-6.
 1993 *Schizorhiza* cf. *weileri* Serra; Welton and Farish, p. 145, figs. 1, 2.

Diagnosis. As for genus.

Material. SEPCPV-15/302; isolated rostral tooth from basal Rancho Nuevo Formation, Difunta Group (Uppermost Maastrichtian) in Canyon El Barril, Coahuila, Mexico. SEPCPV-1/303; fragmentary rostrum with intact rostral tooth battery preserved in siderite concretion from about 120 meters above the base of the Cerro de Pueblo Formation, Difunta Group (Uppermost Campanian) at Rincón Colorado, Coahuila, Mexico. Other partial rostra

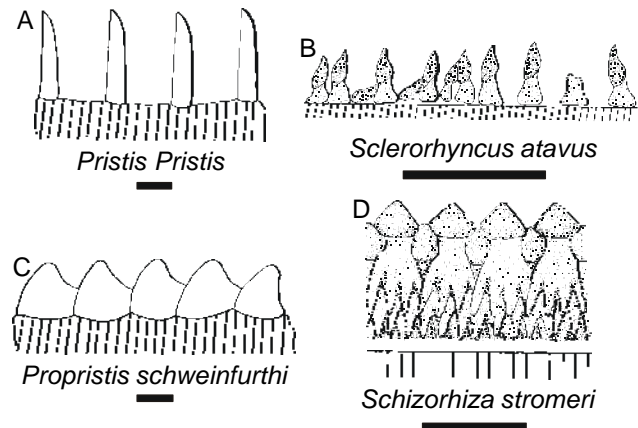


Figure 9. Lateral view of part of the rostral tooth row of various sawfish. A) and B) comb-like rostra: A) modern sawfish *Pristis pristis*; B) sclerorhynchid sawfish *Sclerorhynchus atavus*. C) and D) saw-like rostra: C) extinct sawfish *Propristis schweinfurthi*; D) sclerorhynchid sawfish *Schizorhiza stromeri*. Scale bars = 1 cm.

lacking associated rostral teeth also from Cerro de Pueblo Formation, Difunta Group (Uppermost Campanian) at Rincón Colorado, Coahuila, Mexico.

Discussion. Cappetta (1987a) only recognizes one species based on tooth morphology. This view is followed here. It is recognized that any variability in rostral tooth morphology would be limited to the efficiency of packing of these elements into the rostral tooth battery. If more complete material is ever recovered, it may well be determined that species characters are reflected more by post-cranial characters such as fin shape and position.

Occurrence. Known only from the upper Campanian through uppermost Maastrichtian (very questionably in the basal Paleocene) in the Tethian region with occurrences across North Africa (Weiler, 1930; Arambourg, 1952; Cappetta, 1991), central Africa (Darteville and Casier, 1943; Cappetta, 1972, 1975), Iraq (Cappetta, 1987a), Italy (Serra, 1933), Bolivia (Cappetta, 1975), Texas, USA (Dunkle, 1948; Welton and Farish, 1993) and Coahuila, Mexico.

CONCLUSIONS

1. The rostrum of *Schizorhiza* is similar to that of other known Sclerorhynchidae species in its gradual taper and in that superficial ophthalmic nerves run down the dorsal grooves and the buccopharyngeal nerves run down the ventral grooves.
2. The arrangement of the rostral teeth of *Schizorhiza* into densely packed files to produce a continuous sharp serrated edge down each side of the rostrum is unique among the Sclerorhynchidae. The development of this sharp serrated edge indicates a specialization toward slashing at prey in open water.

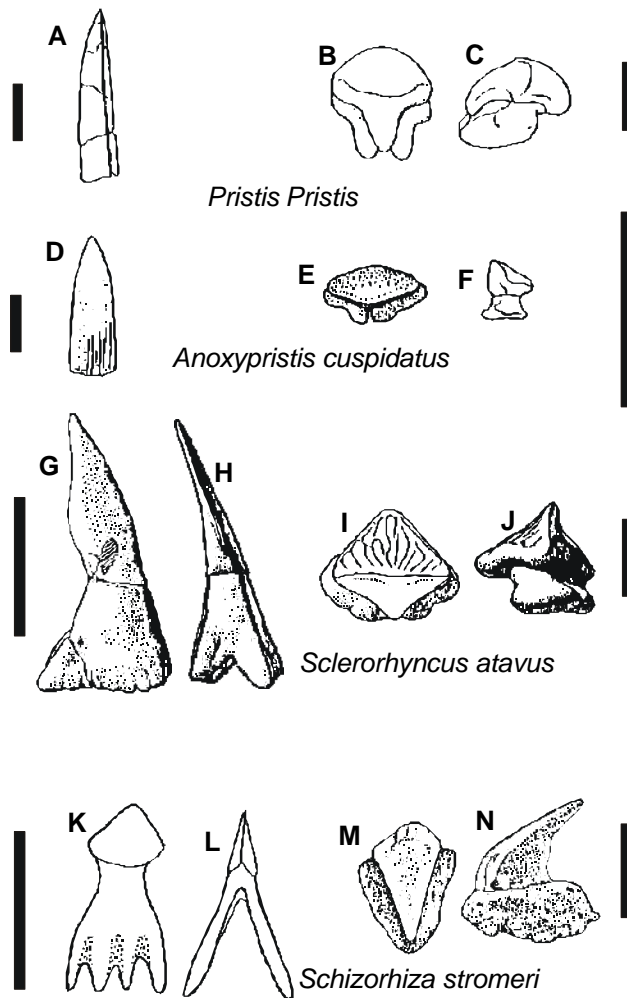


Figure 10. Rostral and oral teeth of sawfish. A-C *Pristis pristis*: A) rostral tooth in dorsal view, B) oral tooth in dorsal view, C) oral tooth in lateral view. D-F *Anoxypristis cuspidatus*: D) rostral tooth in dorsal view, E) oral tooth in dorsal view, F) oral tooth in lateral view. G-J *Sclerorhynchus atavus*: G) rostral tooth in dorsal view, H) rostral tooth in posterior view, I) oral tooth in dorsal view, J) oral tooth in lateral view. K-N *Schizorhiza stromeri*: K) rostral tooth in dorsal view, L) rostral tooth in posterior view, M) oral tooth in dorsal view, N) oral tooth in lateral view. Scale bars for rostral teeth = 1 cm. Scale bars for oral teeth = 1 mm.

3. The occurrence of *Schizorhiza* in the Rancho Nuevo Formation suggests that either this taxon survived into the basal Paleocene or that the Cretaceous-Tertiary boundary is stratigraphically higher than indicated by previous research. Although thought to be in place, it is possible that this specimen is reworked from older strata.

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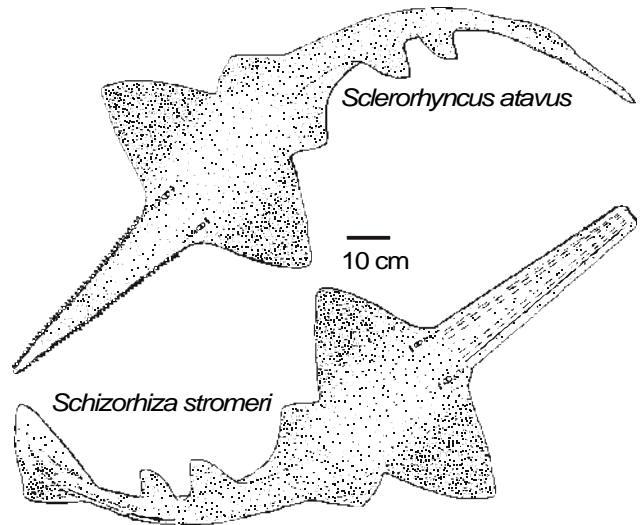


Figure 11. A.) Reconstruction of *Sclerorhynchus atavus* based on illustrations in Cappetta (1980). This taxon would appear to have been a benthonic taxon. B.) Hypothetical reconstruction of *Schizorhiza stromeri* as a more pelagic taxon with a more lunate tail.

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