PALEOBIOLOGY AND PALEOBIOGEOGRAPHY OF SCLERORHYNCHID SAWFISHES (CHONDRICHTHYES, BATOMORPHII)

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ABSTRACT

Sclerorhynchid sawfishes are a monophyletic group of Cretaceous selachians. They resemble modern sawfishes in the outer morphology and by having a hypertrophic rostral cartilage armed with lateral rows of spines. Generally, sclerorhynchid sawfishes were inhabitants of warm, shallow tropical and subtropical marine environments. Teeth of the oldest sclerorhynchid sawfishes from Spain are presented. They belong to *Onchopristis* Stromer and come from the lower Barremian of eastern Spain. The paleobiology and paleogeographic pattern of sclerorhynchid sawfishes is reviewed and discussed.

Keywords: Sclerorhynchidae, Batomorphii, paleobiology, paleobiogeography.

RESUMEN

Los peces sierra esclerorrínquidos forman un grupo monofilético de seláceos cretácicos. Se asemejan a las formas actuales de peces sierra en la morfología externa y en la presencia de un cartílago rostral hipertrófico armado con filas laterales de espinas. La paleta rostral fue usada de la misma manera que los prístidos actuales. Generalemente los esclerorrínquidos habitaron medios tropicales y subtropicales de aguas someras y cálidas. Se presentan en este trabajo los dientes de *Onchopristis* Stromer, el más antiguo esclerorrínquido de España. Así mismo se discute la paleobiología y patrones de distribución de los peces sierra esclerorrínquidos.

Palabras clave: Sclerorhynchidae, Batomorphii, paleobiología, paleobiogeografía.

INTRODUCTION

Sclerorhynchid sawfishes are a monophyletic group of extinct batoid fishes. They resemble modern sawfishes of the family Pristidae by having a long and slender body with ventral gill slites, pectorals attached to the head and a hypertrophic rostrum forming a rostral blade which is armed with lateral rows of rostral spines (Fig. 1). Generally, sclerorhynchids are placed within Rajiformes on subordinal rang (Sclerorhynchoidei Cappetta, 1980). So far, Sclerorhynchoidei comprises a single family, Sclerorhynchidae, which was errected by Cappetta (1974). The oldest sclerorhynchid remains (isolated oral teeth) are from the Early Cretaceous of Europe, North Africa and North America (*e.g.*, lower Barremian of Spain, Kriwet (1999), Albian of northern Africa, Haug (1905), Stromer (1927); Aptian-Albian boundary of Texas, Thurmond (1971), Branch and Mosley (1997). At least 16 genera with at least 40 species have been described up to now which are only restricted to the Cretaceous period. The most common Early Cretaceous sclerorhynchid sawfish is *Onchopristis* Stromer, 1917. Although most sclerorhynchids are known by isolated rostral or oral teeth only, Upper Cretaceous sediments of Egypt yielded well preserved rostral blades. Furthermore, articulated skeletons of several genera are known from the Cenomanian and Santonian of Lebanon (Cappetta, 1980).

Similar neoselachian sharks evolved convergently. The sawsharks (Pristiophorifomes) first appeared in the

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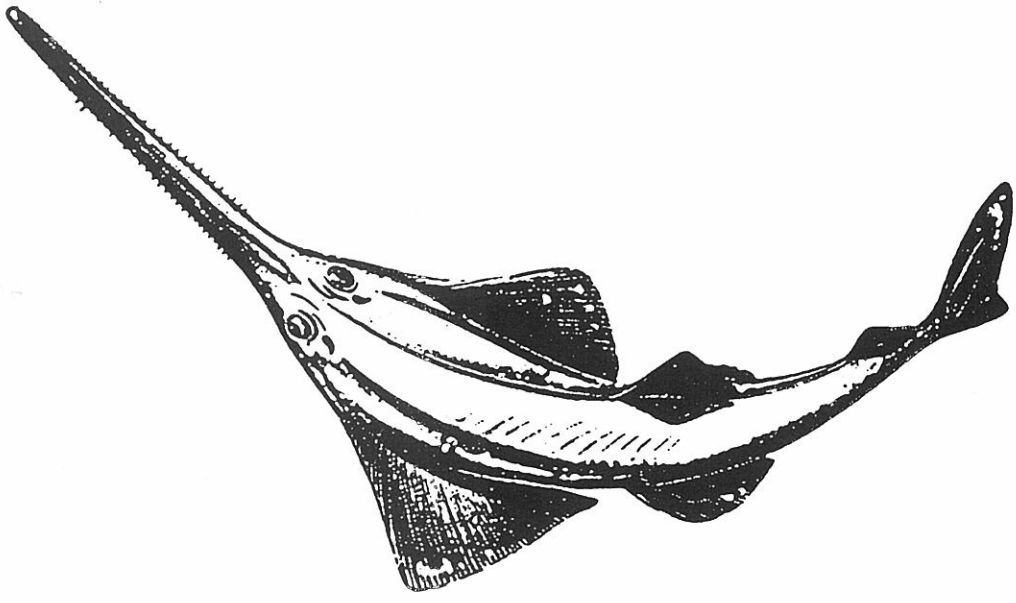

Figure 1. Outline restoration of a Cretaceous sclerorhynchid sawfish. Redrawn from Frickhinger (1991) with permission.

Santonian of Lebanon. Weiler (1935) attributed isolated remains from the Cenomanian of Egypt as *Peyeria libyca* (Weiler, 1935) to pristid sawfishes (Pristiformes). However, these remains may represent more likely dermal thorns of any batoid (Cappetta, 1987). Pristids first appeared in the Palaeogene.

The aim of the present paper is to give a review of the paleobiology and paleogeographic distribution of sclerorhynchids and to present the oldest sclerorhynchid sawfish remains from Spain.

PALEOBIOLOGY OF SCLERORHYNCHID SAWFISHES

Sclerorhynchid sawfishes most likely occupied an ecological niche equivalent to that presently filled by pristid sawfishes and pristiophorid sawsharks (Welton and Farish, 1993). Like Recent pristids, sclerorhynchids were mainly sluggish bottom dwellers of shallow near-coast waters, of bays and estuaries. Some were probably capable to ascend into freshwaters like Recent pristids that intrude the Nicaragua lake and freshwaters in Sambesi (*e.g.*, Bigelow and Schroeder, 1953). The sclerorhynchid sawfishes *Ischyrhiza* Leidy, *Dalpiazia* Checchia-Rispoli and *Schizorhiza* Weiler were interpreted as nectonic fishes by Cappetta (1972, 1980). Most sclerorhynchids show a rather limited distribution. But at least four genera are cosmopolitan and some others are distributed over large distances (Tab. 1). Werner (1989) considered the sclerorhynchids *Micropristis* Cappetta, 1980 and *Libanopristis* Cappetta, 1980 as batoids of deeper water regions whereas *Onchopristis* Stromer, 1917, *Bahariprístis* Werner, 1989 and *Marckgrafia* Weiler, 1935 were confined to coastal waters. Branch and Mosley (1997) concluded that sclerorhynchids frequented warm, shallow tropical marine environments like Recent pristids.

The function of the rostral blade of sclerorhynchids (Fig. 2) is still discussed. The assumption that it was used to probe into sand or mud to dig up small invertebrates or fish whatever they were able to catch like Recent pristids may do nowadays is not verified. Only few rostral spines of sclerorhynchids show the typical abrasion pattern as found on rostral spines of Recent pristids (Fig. 3). This may be due to the early loss of damaged spines (Slaughter and Springer, 1968) or that the rostral blade was not used for grubbing in sand or mud. Another possibility is that sclerorhynchids mainly used the rostral blade to paralyze or kill small fishes or invertebrates like crays by slashing the blade to and fro in schools of fish (*e.g.*, Welton and Farish, 1993). But Recent pristids do not show this adaption. They catch prey like other sharks and rays without the help of the rostral blade (Schultze, pers. com.). More convincing is the assumption that the rostral blade represents a powerfull weapon.

The oral dentition is of crushing-type ("type ecraseur" of Cappetta, 1986) indicating shelled food like bivalves or crustaceans in addition to small fish.

ONCHOPRISTIS STROMER IN THE LOWER CRETACEOUS OF ALCAINE, EASTERN SPAIN

Onchopristis is common in the Lower and Middle Cretaceous of Europe, North Africa and the U.S.A. The oldest sclerorhynchid sawfish remains come from marly sediments of early Barremian age near the village of Alcaine, Province of Teruel of Spain and consist of isolated oral teeth (Fig. 4; Kriwet, 1999). The vertebrate bearing strata of Alcaine are located within the Oliete subbasin in the central Iberian Ranges. The sedimentation of the basin was mainly alluvial and continental with

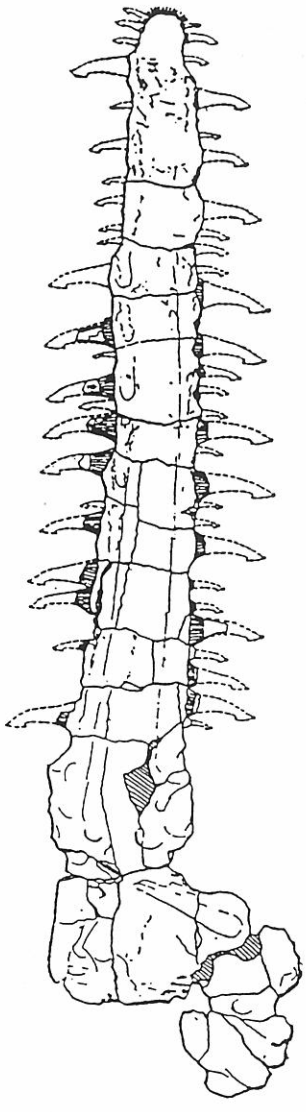

Figure 2. Rostral blade of *Onchopristis numidus* Haug, 1905 from the Cenomanian of Egypt. Taken from Arambourg (1940).

Wealden facies interbedded with shallow marine, lagoonal sediments. The teeth were recovered in marine influenced strata. This interpretation is also confirmed by the occurrence of a diverse near-coast selachian fauna and teeth of two semi-aquatic crocodilians, *Bernissartia* and *Theriosuchus*.

Onchopristis is characterized by a rather thick rostral blade in comparison to other sclerorhynchids. The teeth are cuspidate with a typical crusiform morphology. The root is of batoid type. The thick rostral blade and the tooth morphology are plesiomorphic within sclerorhynchids (Kriwet, in prep.).

The material from Alcaine comprises five isolated oral teeth which are attributed to *Onchopristis dunklei* McNulty and Slaughter (Fig. 4, A-F) (Measurements: mesio-distal width of teeth: 0.7-1.1 mm; height of teeth: 0.75-1.2 mm) and *Onchopristis* sp. (Fig. 4, G-H) (Measurements: mesio-distal width of tooth crown: 0.73 mm; height of tooth crown: 1.35 mm).

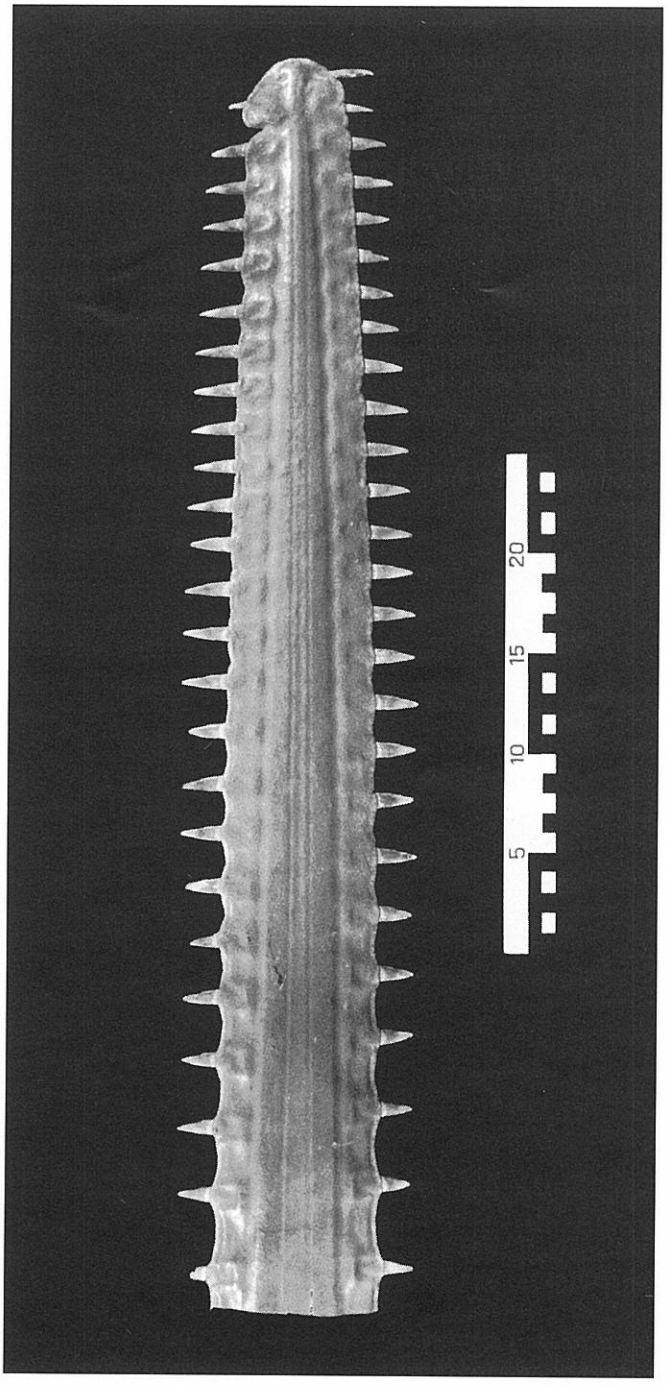

Figure 3. Rostral blade of the Recent pristid sawfish *Pristis pectinata* Latham.

PALEOBIOGEOGRAPHY OF SCLERORHYNCHID SAWFISHES

To reconstruct the paleobiogeography of sclerorhynchid sawfishes nearly 200 citations from about 90 papers were considered. The distribution was coded stratigraphically to different areas: Arabia, India, Eurasia (mainly Kazakhstan), Near and Middle East (Syria, Israel, Iraq, Lebanon, Jordania), Europe, northern Africa (Marocco, Algeria, Tunisia, Lybia, Egypt), Africa (Angola, Cabinda, Niger, Nigeria, Zaire), North America

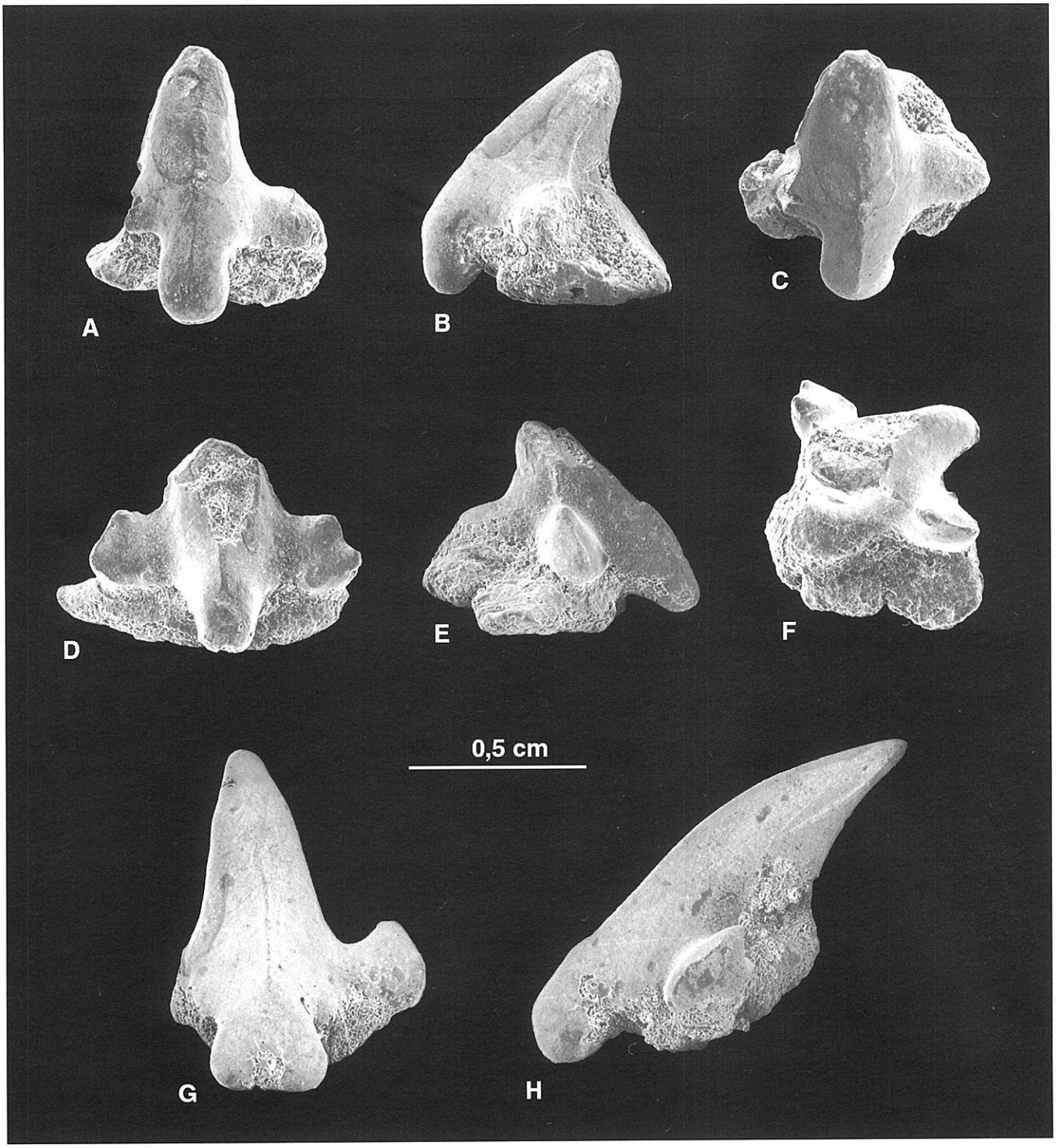

Figure 4. Isolated oral teeth of *Onchopristis* Stromer, 1917 from the lower Barremian of Alcaine, Province of Teruel. **A-C:** Anterior tooth of *Onchopristis dunklei*. **A:** Labial view. **B:** Lateral view. **C:** Occlusal view. **D-F:** Lateral tooth *Onchopristis dunklei*. **D:** Labial view. **E:** Lateral view. **F:** Occlusal view. **G-H:** Tooth of *Onchopristis* sp. **G:** Labial view. **H:** Lateral view.

(U.S.A. and Canada), South America (Brazil, Bolivia, Chile, Ecuador, Peru), and the Pacific area (Japan and New Zealand). The summary of this investigation is shown in Tab. 1 and in Appendix 1. The qualitative distribution of sclerorhynchid genera is shown in Fig. 5. Unfortunately, space preludes an extensive discussion of the distributional patterns of sclerorhynchids. Therefore, we give only some general conclusions.

The oldest known sclerorhynchid, *Onchopristis*, is from the lower Barremian of Europe. Other Early Cretaceous records are from the Aptian-Albian boundary of Texas (*Onchopristis praecursor* and *Onchopristis* sp.;

Genus	Europe	Greenland	Near East	North Africa	Africa
Ankistrorhynchus	Sa				
Baharipristis				Ce	
Borodinopristis					
Ctenopristis			Ma	Ma, Th?*	Ma
Dalpiazia			Ma	Ma	Ma
Ganopristis	Ma		Ca/Ma	Ma	
Ischyrhiza	Sa, Pa*				Ma
Libanopristis			Ce		
Marckgrafia				Ce	
Micropristis	Sa?, Ca?		Ce		
Onchopristis	Ba, Ce	Ce/Tu (?)		Al, Ce, Sa, Ca	
Onchosaurus	Sen			Sa	Tu, Sen
cf. *Onchosaurus*					
Plicatopristis			Ma	Ma	
Pucapristis					
Schizorhiza			Ma	Ma	Ma
Sclerorhynchus	Ma, Pa*		Sa, Ca	Sen	
Sclerorhynchidae indet.	Co, Ca				

Genus	North America	South America	Pacific area	Eurasia	India	Arabia
Ankistrorhynchus	Ca, Ma					
Baharipristis						
Borodinopristis	Sa, Ca					
Ctenopristis						
Dalpiazia						
Ganopristis						
Ischyrhiza	Ce/Tu - Ma, Mo?*	Ca?, Ma	Co/Sa	Tu - Ca		
Libanopristis						
Marckgrafia						
Micropristis						
Onchopristis	Ap/Al, Ce, Ca				Upp. Cret.	
Onchosaurus	Ca	Tu, Sen				
cf. *Onchosaurus*	Sa					
Plicatopristis						
Pucapristis		Ma, Pa?**				
Schizorhiza	Ma	Ca, Ma				
Sclerorhynchus	Tu/Co, Ce, Ca, Ma	Ca	Ca/Ma			Upp. Cret.
Sclerorhynchidae indet.		Ca/Ma				

Abbreviations:

Ba = Barremian	Ca = Campanian
Ap = Aptian	Ma = Maastrichtian
Al = Albian	Mo? = Montian
Ce = Cenomania	Pa, Pa? = Paleocene
Tu = Turonian	Sen = Senonian
Co = Coniacian	* = reworked
Sa = Santonian	** = no sclerorhynchid

Table 1. Paleogeographic and stratigraphic distribution of sclerorhynchid sawfishes.

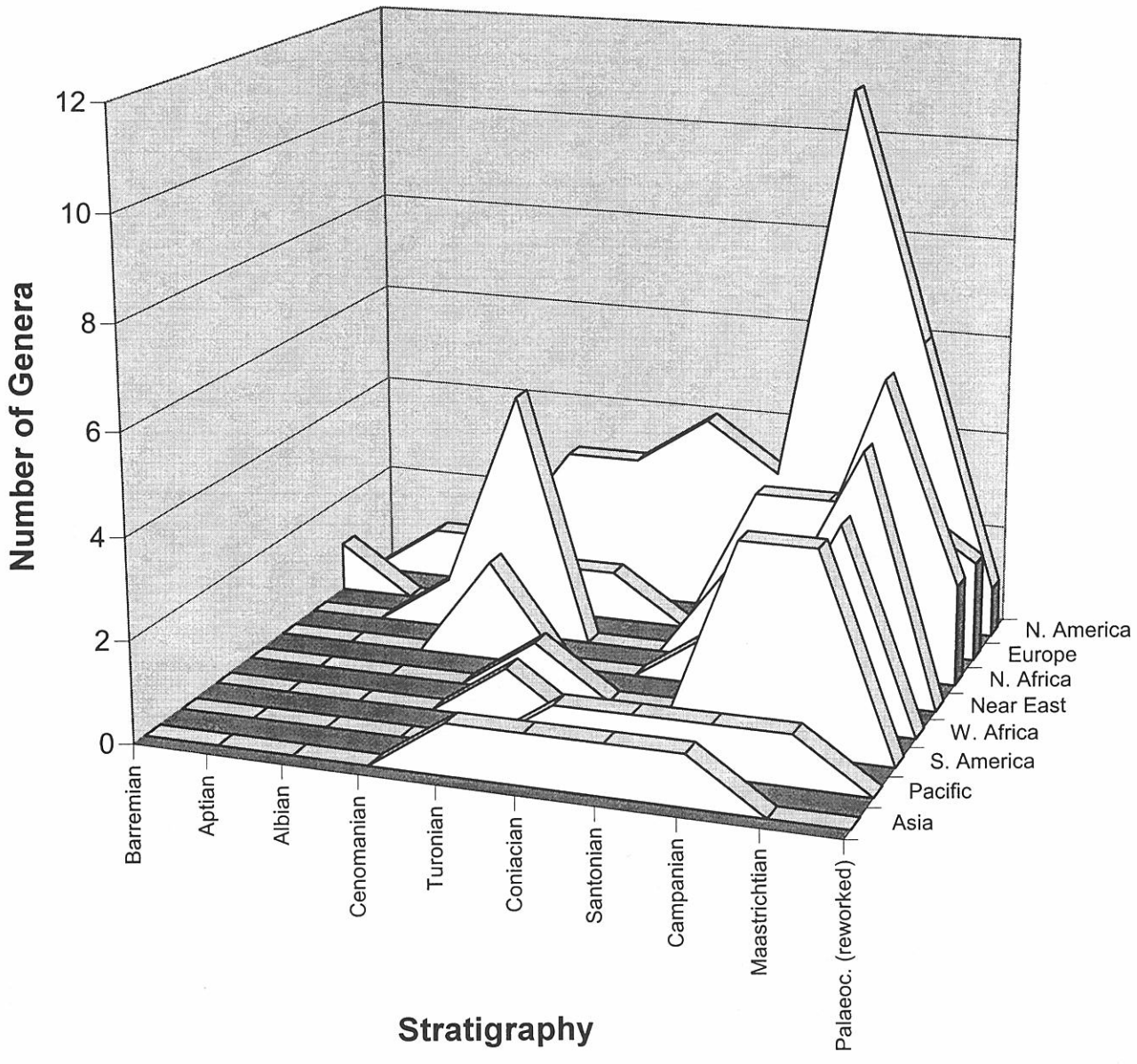

Figure 5. Qualitative distribution of sclerorhynchid sawfish genera. Numbers on the y-axis represent numbers of genera.

Thurmond, 1971, 1974; Cappetta *et al.*, 1993; Branch and Mosley, 1997). *Onchopristis* is also common in upper Albian and Cenomanian strata of northern Africa (Fig. 6), in the Lower and Upper Cretaceous of the U.S.A., rocks close to the Cenomanian-Turonian boundary of Greenland, and in the Cenomanian of Egypt (*e.g.*, Cappetta and Case, 1999; Haug, 1905; Slaughter and Steiner, 1968; Stromer, 1925; Werner, 1989). *Onchopristis* was assumed to be the only representative of sclerorhynchid sawfishes in the Early Cretaceous. Nevertheless, a rostral spine identified as sclerorhynchid remain was recently reported from the upper Albian of England (Underwood and Mitchell, 1999). The specimen differs from rostral spines of *Onchopristis*. Moreover, the peculiar morphology is not characteristic for sclerorhynchid rostral spines (Cappetta, pers. com.).

In the Cenomanian, sclerorhynchid sawfishes are more diverse. At least six sclerorhynchid genera are known in the Cenomanian of France (*Onchopristis*), Lebanon (*Libanopristis*, *Micropristis*), North Africa (*Baharipristis*, *Marckgrafia*, *Onchopristis*), and North America (*Onchopristis*, *Sclerorhynchus*) (e.g., Cappetta, 1980; Cappetta, 1987; Werner, 1989; Case, 1991).

Sclerorhynchid sawfish records from the Turonian and Coniacian are rather rare. Most common is *Ischyrhiza*. Other Turonian and Coniacian sclerorhynchids are *Onchopristis*, *Onchosaurus* and *Sclerorhynchus* (*e.g.*, Dunkle, 1951; Cappetta and Case 1999). The oldest record of *Ischyrhiza*, perhaps the most succesful sclerorhynchid, is from the Cenomanian-Turonian boundary of Arizona (Williamson *et al.*, 1993). *Ischyrhiza* is a common element of Upper Cretaceous elasmobranch faunas of the U.S.A. Outside North America *Ischyrhiza* species were found in the Coniacian/Santonian of Japan (Uyeno and Hasegawa, 1986; Goto *et al.*, 1996), the Campanian of northwestern

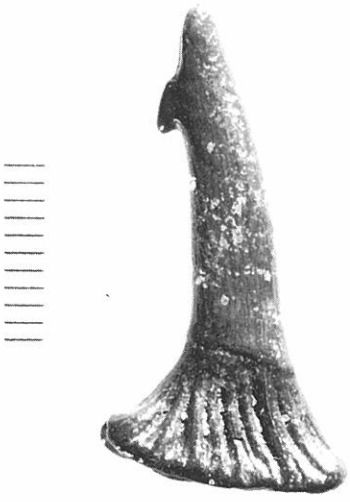

Figure 6. Rostral spine of *Onchopristis numidus* Haug, 1905 from the Cenomanian of Morocco, dorsal view. Scale bar in millimeter.

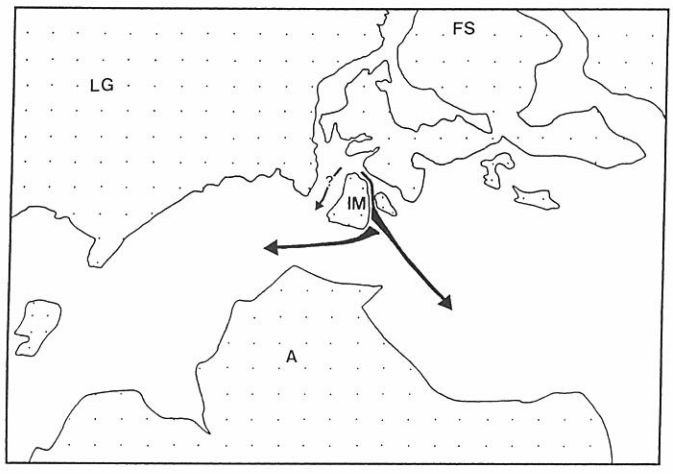

Figure. 7. Barremian-Hauterivian paleogeographic map showing the early diversification of sclerorhynchid sawfishes. The centre of diversification is located somewhere in Middle Europe. During the Lower Cretaceous sclerorhynchids spread along the coast of Iberia to the south and west. Base map from Smith *et al.* (1994). **A** = Africa, **FS** = Fennosarmatia, **IM** = Iberian Massif, **LG** = Laurentia-Greenland.

Germany, described as *Sclerorhynchus germaniae* by Albers and Weiler (1964), the Santonian of France (Cappetta, 1981), the Maastrichtian of Bolivia (Cappetta, 1975), and the Maastrichtian of Niger (Cappetta, 1972).

The record of sclerorhynchid sawfishes from the Santonian seems to be rather incomplete. Only seven identified species and a specimen of uncertain affinity were reported from five countries (Appendix 1). One of these species, *Sclerorhynchus atavus*, is represented by several well preserved specimens from limestones of Lebanon (Woodward, 1892; Cappetta, 1980, 1987).

In the Campanian, sclerorhynchid sawfishes are known mainly from the U.S.A. Other Campanian sclerorhynchids were reported from Kazakhstan (Glikman, 1967), Germany (Müller, 1989), Israel (Lewy and Cappetta, 1989) and from Peru (Mourier *et al.*, 1988). There are about 30 regional citations in the Campanian indicating the occurence of at least 11 species and several specimens without specific determination.

The Maastrichtian marks the peak of the distribution and evolution of sclerorhynchids. At least 15 species belonging to nine genera are cited from a total of 42 areas. Unfortunately, there are several citations without specific identification of the remains or inaccurate stratigraphic assignments. These citations were not further considered.

Recently, Smith (1999) documented an isolated rostral spine of *Ischyrhiza* sp. and an isolated oral tooth of *Sclerorhynchus* sp. cf. *S. pettersi* Case and Cappetta, 1997 from upper Paleocene strata of Belgium. However, this rostral spine is reworked from Upper Cretaceous strata (Cappetta, pers. com.). If the stratigraphy is correct these remains indicate the survival of sclerorhynchids across the Cretaceous/Tertiary boundary.

North America (including Canada and the U.S.A.) reveals the greatest diversity (about 62 citations from the uppermost Aptian to the Maastrichtian, 27 citations alone in Texas), followed by North Africa with about 23 citations ranging from the upper Albian to the Maastrichtian.

In contrast, only a single species was reported from the following regions: Arabian Peninsula (*Sclerorhynchus* sp., Upper Cretaceous); Algeria, North Africa [*Onchopristis numidus* (Haug, 1905), upper Albian]; Cabinda, Africa (*Ctenopristis nougareti* Arambourg, 1940, Maastrichtian); Nigeria, Africa (*Schizorhiza stromeri* Weiler, Maastrichtian); Alberta, Canada (*Ischyrhiza mira* Leidy, Campanian); North Carolina, U.S.A. (*Ischyrhiza mira* Leidy, Maastrichtian); South Dakota, U.S.A. (*Ischyrhiza avonicola* Estes, Turonian); Brazil, South America [*Onchosaurus pharao* (Dames), Senonian]; Chile, South America (*Schizorhiza stromeri* Weiler, 1930, Maastrichtian); Ecuador, South America (*Onchosaurus* cf. *radicalis*, Turonian) and from New Zealand, Pacific area (*Sclerorhynchus*? sp. identified as *Onchopristis dunklei praecursor* by Keyes (1977), Campanian-Maastrichtian). Eurasia, Asia and the Pacific area are poor in sclerorhynchid sawfish remains. But this may represent a collecting bias.

The occurrences of sclerorhynchid sawfishes can be divided into three zoogeographic zones (Tab. 2): **1.** Cosmopolitan sawfishes: *Ischyrhiza*, *Onchopristis*, *Onchosaurus* and *Sclerorhynchus*. **2.** Endemic Laurasian (North America, Europe and Eurasia and Asia north of the Himalaya) sawfishes: *Ankistrorhynchus* and *Borodinopristis*. **3.** Endemic Gondwanan (South America, Africa, Madagaskar, India, Arabia, Malaya, Australia, Antarctica) sawfishes: *Baharipristis*, *Ctenopristis*, *Libanopristis*, *Marckgrafia*, *Micropristis* (occurs probably also in the Upper Cretaceous of Europe, see Appendix 1, Cappetta, 1987), *Plicatopristis* Cappetta, 1991 and *Pucapristis* Schaeffer. *Ganopristis* Arambourg

Gondwana sawfishes	Laurasian sawfishes	Cosmopolitan sawfishes
Baharipristis	*Ankistrorhynchus*	*Ganopristis*
Ctenopristis	*Borodinopristis*	*Ischyrhiza*
Libanopristis		*Onchopristis*
Marckgrafia		*Onchosaurus*
Micropristis		*Schizorhiza*
Plicatopristis		*Sclerorhynchus*
Pucapristis		

Table 2. Zoogeography of sclerorhynchid sawfishes.

is mainly restricted to Africa but was also found in the Maastrichtian of the Netherlands (Casier, 1964) and Northern Spain (Cappetta and Corral, 1999). In addition, *Dalpiazia*, mainly known from Gondwana, also occurs in the Maastrichtian of Northern Spain (Cappetta and Corral, 1999). The mainly Gondwanan sclerorhynchid *Schizorhiza* was also reported from the Maastrichtian of Texas, U.S.A. (Dunkle, 1948). Therefore, both genera can be assigned to the cosmopolitan group.

Cosmopolitan sawfishes are defined as group with distribution on the northern and southern hemisphere. About 37.5% of all sclerorhynchid genera belong to this group (including *Ganopristis* and *Schizorhiza*). *Ischyrhiza* is a typical faunal element of the North American Gulf coastal plains and the interior seaway, but it is also known from Europe, Japan and South America. Half of all known sclerorhynchid sawfishes (= 50%) can be attributed to the Gondwanan group.

There is only minor evidence favouring an interchange between South America and Africa. A pattern of sympatry emerges in the Turonian, Campanian and Maastrichtian if the records of *Ischyrhiza*, *Onchosaurus*, *Schizorhiza* and *Sclerorhynchus* are considered.

Endemic sawfishes of North and South America are *Borodinopristis* and *Pucapristis* respectively (Case, 1987; Cappetta, 1987). *Pucapristis* may have even biostratigraphic value. Other Gondwanan sawfishes of South America are *Onchosaurus* (Turonian of Ecuador and Maastrichtian of Brasil, Cappetta, 1987) and to some extend *Schizorhiza* (Maastrichtian of Bolivia). But *Schizorhiza* also occurs in Iraq and Jordania (JK, pers. obs.).

Africa shows the greatest diversity of endemic sawfishes. About 21% can be attributed to this group.

Only two sclerorhynchids have a Laurasian distribution pattern (= 12.5%; see above).

Sclerorhynchid sawfishes are rarely known from the Middle East (Iraq, Jordan, Lebanon), India, Japan and from Eurasia, especially from the former U.S.S.R. Nessov (1997) indicates the occurrence of a new species of *Ischyrhiza*, *I. serra*, in the upper Turonian and Coniacian and perhaps in the Santonian of Uzbekistan. Probably a new species of *Ischyrhiza* was found in the lower Campanian of Kazakhstan and identified by Glikman (1980) as *Onchosaurus* sp. (Averianov, pers. com.). Recently, a first summary of Syrian selachians from the uppermost Cretaceous was published by Bardet *et al.* (2000) including references on sclerorhynchid sawfishes.

CONCLUSIONS

Sclerorhynchid sawfishes are known from many Lower and Upper Cretaceous marine fossil localities. They are batoids with a dorso-ventrally flattened body, with pectorals attached to the head and a long hypertrophic rostrum armed with lateral rows of specific spines. In comparison with Recent pristid sawfishes it is assumed that they mainly lived near the bottom in shallow water with sandy or muddy substrate. The rostral blade was certainly used in many ways. It is assumed that

Stratigraphy	Europe	Greenland	Near East	North Africa	Africa	North America	South America	Pacific area	Eurasia
Paleocene	Is?, S?								
Maastrichtian	Ga, S		Ct, Ga, Sc, Da, Pl	Ba, Ct, Da, Ga, Pl, Sc	Ct, Da, Is, Sc	Ma, Is, Sc, S	Is, Pu, Sc	S	
Campanian	Mi?		Ga, S	O		An, Bo, Is, O, On, S	Is?, On, S	S	Is
Santonian	An, Is, Mi?		S	O, On		Bo, Is, On?		Is	Is
Coniacian						Is, S		Is	Is
Turonian		O			On	Is, S	On		Is
Cenomanian	O	O	Li, Mi	Ma, O		Is, O, S			
Albian	Scl			O		O			
Aptian						O			
Barremian	O								
Hauterivian	O								

Abbreviations:

An = *Ankistrorhynchus*	Ma = *Marckgrafia*	Scl = Sclerorhynchidae indet.
Ba = *Baharipristis*	Mi = *Micropristis*	
Bo = *Borodinopristis*	O = *Onchopristis*	
Ct = *Ctenopristis*	On = *Onchosaurus*	
Da = *Dalpiazia*	Pl = *Plicatopristis*	
Ga = *Ganopristis*	Pu = *Pucapristis*	
Is = *Ischyrhiza*	Sc = *Schizorhiza*	
Li = *Libanopristis*	S = *Sclerorhynchus*	

Table 3. Distribution of sclerorhynchid sawfishes showing similarities between areas.

it was used to grub for food into the sediment or to slash it into schools of fish to kill the prey. However, the spines show minor or no abrasion compared to rostral spines of extant pristids. This may contradict the interpretation that the rostral blade was used to grub into the sediment. Additional, the blade certainly also served as a weapon for defense and/or offense. The oral tooth morphology indicates that they fed on small fish and shelled invertebrates like crustaceans or echinoderms like most Recent rajiform batoids.

An analysis of the biogeographical distribution of fossil organisms may be best carried out by calculating faunal similarities for different areas using similarity coefficients (e.g., Simpson index, Jaccard index, Johnson index). But to obtain useful and good results the faunal compositions should include many different species (> 25). For the batoid group discussed in this paper the application of such statistical approaches is not useful as the faunal compositions of the investigated areas are too small on specific level (see Appendix 1).

The earliest known sclerorhynchid representative belongs to the genus *Onchopristis* and comes from the Hauterivian of England and Barremian of Spain (Tab. 3). *Onchopristis* seems to be absent in the Aptian and Albian of Europe. But this may be due to a collecting bias. The only Albian sclerorhynchid of Europe was reported in open nomenclature from England. Outside Europe, *Onchopristis* is found in the Aptian and Albian to Cenomanian of Texas (U.S.A.). The Cenomanian represents the first peak of sclerorhynchid distribution (Tab. 3). Seven species belonging to seven genera are knwon from Europe, Near East, North Africa and North America. The Aptian/Albian and Cenomanian records of sclerorhynchids from the Near East, North Africa and North America prove a rapide diversification of sclerorhynchids during the Early Cretaceous and Cenomanian. The centre of origin and diversification is located somewhere in the Tethys area of Middle Europe (Fig. 7). So far, the ancestor of sclerorhynchids is not known.

The Cenomanian of Egypt and Lebanon is marked by several endemic genera (e.g., *Bahariprístis*, *Marckgrafia*, *Libanopristis*). The most succesful sclerorhynchid, *Ischyrhiza*, first appeared in the Cenomanian of North America and is quite common in the Turonian and Coniacian of the western Tethys and the Interior Sea way of North America. The rather rare records of Coniacian sclerorhynchids (almost all belong to *Ischyrhiza*) are related to the absence of possible sediments to collect. The Campanian and Maastrichtian represents the second peak of sclerorhynchid distribution (Tab. 3). Sclerorhynchids are restricted mainly to the Cretaceous period. The rare occurrences in the Lower Tertiary are either reworked specimens (e.g., *Ctenopristis nougareti* from the Thanetian of Marocco and *Ischyrhiza mira* from the Montian of Texas) or belong to other elasmobranchs, e.g., *Pucapristis*? *standhardtae* Williamson and Lucas, 1993 from the Paleocene of New Mexico, U.S.A., which may belong in fact to an orectolobid shark and *Sclerorhynchus palaeocenicus* from the Paleocene of Marocco (Herman, 1973) which must be attributed to *Pristiophorus* (Cappetta, 1987). Reworked remains of two sclerorhynchid sawfishes were recently reported from the upper Paleocene of Belgium (Smith, 1999). The radiation of sclerorhynchids in the Cretaceous is supported by high sea levels during transgressive phases (e.g., Cenomanian transgression), lack of barriers to migration, and low latitudinal gradients during the Cretaceous period. Separated Boreal and Tethyal elasmobranch faunal provinces were postulated by Werner (1989) based on the distribution of batoid species (contra Williamson *et al.*, 1993). Our investigations also do not confirm the results of Werner (1989).

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Appendix 1. Occurrences of sclerorhynchid sawfishes

Genus	Species	Stratigraphy	Region	Continent
Ankistrorhynchus	*lonzeensis*	Santonian	Belgium	Europe
Ankistrorhynchus	*major*	Maastrichtian	New Jersey	N. America
Ankistrorhynchus	*washakiensis*	Campanian	Wyoming	N. America
Bahariprístis	*bastetiae*	Cenomanian	Egypte	N. Africa
Borodinopristis	*schwimmeri*	Campanian	Georgia	N. America
Borodinopristis	*schwimmeri*	Santonian	Mississippi	N. America
Borodinopristis	*schwimmeri*	Campanian	Mississippi	N. America
cf. Onchosaurus	sp.	Santonian	New Mexico	N. America
Ctenopristis	*nougareti*	Maastrichtian	Angola	W. Africa
Ctenopristis	*nougareti*	Maastrichtian	Cabinda	W. Africa
Ctenopristis	*nougareti*	Maastrichtian	Irak	Near East
Ctenopristis	sp.	Maastrichtian	Syria	Near East
Ctenopristis	*nougareti*	Maastrichtian	Morocco	N. Africa
Ctenopristis	*nougareti*	Thanet (Redeposition)	Morocco	N. Africa
Ctenopristis	*nougareti*	Maastrichtian	Zaire	W. Africa
Dalpiazia	*stromeri*	Maastrichtian	Egypte	N. Africa
Dalpiazia	*stromeri*	Maastrichtian	Libya	N. Africa
Dalpiazia	*stromeri*	Maastrichtian	Morocco	N. Africa
Dalpiazia	*stromeri*	Maastrichtian	Niger	W. Africa
Dalpiazia	*stromeri*	Maastrichtian	Zaire	W. Africa
Dalpiazia	*stromeri*	Maastrichtian	Syria	Near East
Ganopristis	*leptodon*	Campanian-Maastricht.	Israel	Near East
Ganopristis	*leptodon*	Campanian-Maastricht.	Syria	Near East
Ganopristis	*leptodon*	Maastrichtian	Morocco	N. Africa
Ganopristis	*leptodon*	Maastrichtian	The Netherlands	Europe
Ganopristis	*leptodon*	Maastrichtian	Tunisia	N. Africa
Ganopristis	sp.	Campanian	Israel	Near East
Ischyrhiza	*avonicola*	Turonian	Arizona	N. America
Ischyrhiza	*avonicola*	Campanian	Montana	N. America
Ischyrhiza	*avonicola*	Maastrichtian	New Jersey	N. America
Ischyrhiza	*avonicola*	Campanian	New Mexico	N. America
Ischyrhiza	*avonicola*	Turonian	New Mexico	N. America
Ischyrhiza	*avonicola*	Turonian	S. Dakota	N. America
Ischyrhiza	*avonicola*	Turonian-Maastrichtian	Texas	N. America
Ischyrhiza	*avonicola*	Maastrichtian	Wyoming	N. America
Ischyrhiza	*basinensis*	Campanian	Wyoming	N. America
Ischyrhiza	cf. *avonicola*	Campanian	Wyoming	N. America
Ischyrhiza	*germaniae*	Campanian	NW. Germany	Europe
Ischyrhiza	*hartenbergeri*	Maastrichtian	Bolivia	S. America
Ischyrhiza	*iwakiensis*	Coniacian-Santonian	Japan	Pacific
Ischyrhiza	*mira*	Montian (Redeposition)	Texas	N. America
Ischyrhiza	*mira*	Campanian-Maastricht.	Texas	N. America
Ischyrhiza	*mira*	Campanian	Alberta	N. America
Ischyrhiza	*mira*	Campanian	Mississippi	N. America
Ischyrhiza	*mira*	Campanian	Montana	N. America
Ischyrhiza	*mira*	Maastrichtian	N. Carolina	N. America
Ischyrhiza	*mira*	Maastrichtian	New Jersey	N. America
Ischyrhiza	*mira*	Santonian	New Mexico	N. America
Ischyrhiza	*mira*	Coniacian	New Mexico	N. America
Ischyrhiza	*mira*	Turonian	New Mexico	N. America
Ischyrhiza	*mira*	Maastrichtian	Texas	N. America
Ischyrhiza	*mira*	Turonian-Senonian	Texas	N. America
Ischyrhiza	*mira*	Turonian-Maastrichtian	Texas	N. America
Ischyrhiza	*mira*	Campanian	W. Georgia	N. America
Ischyrhiza	*mira*	Campanian	Wyoming	N. America
Ischyrhiza	*monasterica*	Maastrichtian	Texas	N. America
Ischyrhiza	*nigeriensis*	Maastrichtian	Niger	W. Africa
Ischyrhiza	*roessingi*	Campanian	Wyoming	N. America
Ischyrhiza	*schneideri*	Cenomanian-Turonian	Arizona	N. America
Ischyrhiza	*schneideri*	Coniacian	New Mexico	N. America
Ischyrhiza	*schneideri*	Turonian-Coniacian	Texas	N. America
Ischyrhiza	*serra*	Turon.-Coniac., Sant.?	Uzbekistan	Eurasia
Ischyrhiza	sp.	Campanian	Montana	N. America
Ischyrhiza	sp.	Campanian	Montana	N. America
Ischyrhiza	sp.	Campanian	Kazakhstan	Eurasia
Ischyrhiza	sp.	Paleocene (reworked)	Belgium	Europe
Ischyrhiza	*viaudi*	Santonian	W. France	Europe
Isch. or Dalpiazia	sp.	Campanian	Peru	S. America
Libanopristis	*hiram*	Cenomanian	Lebanon	Near East
Marckgrafia	*libyca*	Cenomanian	Egypte	N. Africa
Micropristis	*solomonis*	Santonian	Belgium	Europe
Micropristis	*solomonis*	Cenomanian	Lebanon	Near East
Micropristis?	sp.	Campanian	NW. Germany	Europe
Onchopristis	cf. *dunklei*	Albian	Texas	N. America
Onchopristis	cf. *numidus*	Cenomanian	Texas	N. America
Onchopristis	*d. praecursor*	Aptian/Albian	Texas	N. America
Onchopristis	*dunklei*	Cenomanian	Arizona	N. America
Onchopristis	*dunklei*	Barremian	E. Spain	Europe
Onchopristis	*dunklei*	Cenomanian	Egypte	N. Africa
Onchopristis	*dunklei*	Cenomanian/Turonian	Greenland	Europe
Onchopristis	*dunklei*	Cenomanian	Minesota	N. America
Onchopristis	*dunklei*	Cenomanian?	N. France	Europe
Onchopristis	*dunklei*	Cenomanian	SW. France	Europe
Onchopristis	*dunklei*	Cenomanian	Texas	N. America
Onchopristis	*dunklei*	Cenomanian	Texas	N. America
Onchopristis	*dunklei*	Cenomanian	Texas	N. America
Onchopristis	*dunklei*	Campanian	Texas	N. America
Onchopristis	*dunklei*	Albian-Cenomanian	Texas	N. America
Onchopristis	*dunklei*	Albian	Texas	N. America
Onchopristis	*numidus*	U. Albian	Algeria	N. Africa
Onchopristis	*numidus*	Cenomanian	Egypte	N. Africa
Onchopristis	*numidus*	Cenomanian	Egypte	N. Africa
Onchopristis	*numidus*	Cenomanian	Egypte	N. Africa
Onchopristis	*numidus*	Cenomanian	Morocco	N. Africa
Onchopristis	sp.	Barremian	E. Spain	Europe
Onchopristis	sp.	U. Cretaceous	India	Asia
Onchopristis	sp.	Santonian-Campanian	Libya	N. Africa
Onchopristis	sp.	Aptian	Texas	N. America
Onchosaurus	cf. *radicalis*	Turonian	Ecuador	S. America
Onchosaurus	*pharao*	Senonian	Angola	W. Africa
Onchosaurus	*pharao*	Senonian	Brazil	S. America
Onchosaurus	*pharao*	Santonian	Egypte	N. Africa
Onchosaurus	*pharao*	Turonian	Niger	W. Africa
Onchosaurus	*pharao*	Campanian	Texas	N. America
Onchosaurus	*pharao*	Senonian	Zaire	W. Africa
Onchosaurus	*radicalis*	Senonian	N. France	Europe
Plicatopristis	*strougoi*	Maastrichtian	Egypte	N. Africa
Plicatopristis	*strougoi*	Maastrichtian	Syria	Near East
Pucapristis	*branisi*	Maastrichtian	Bolivia	S. America
Pucapristis	*branisi*	Maastrichtian	Bolivia	S. America
Pucapristis?	*standhardtae*	Paleocene (Misident.)	New Mexico	N. America
Schizorhiza	aff. *stromeri*	Campanian-Maastricht.	Bolivia	S. America
Schizorhiza	cf. *stromeri*	Maastrichtian	Texas	N. America
Schizorhiza	*stromeri*	Maastrichtian	Angola	W. Africa
Schizorhiza	*stromeri*	Maastrichtian	Bolivia	S. America
Schizorhiza	*stromeri*	Maastrichtian	Chile	S. America
Schizorhiza	*stromeri*	Maastrichtian	Egypte	N. Africa
Schizorhiza	*stromeri*	Maastrichtian	Iraq	Near East
Schizorhiza	*stromeri*	Maastrichtian	Jordania	Near East
Schizorhiza	*stromeri*	Maastrichtian	Syria	Near East
Schizorhiza	*stromeri*	Maastrichtian	Libya	N. Africa
Schizorhiza	*stromeri*	Maastrichtian	Morocco	N. Africa
Schizorhiza	*stromeri*	Maastrichtian	Niger	W. Africa
Schizorhiza	*stromeri*	Maastrichtian	Nigeria	W. Africa
Schizorhiza	*stromeri*	Maastrichtian	Texas	N. America
Schizorhiza	*stromeri*	Maastrichtian	Tunisia	N. Africa
Schizorhiza	*stromeri*	Maastrichtian	Zaire	W. Africa
Sclerorhynchus	*atavus*	Santonian	Lebanon	Near East
Sclerorhynchus	*batavicus*	Maastrichtian	Netherlands	Europe
Sclerorhynchus	cf. *pettersi*	Paleocene (reworked)	Belgium	Europe
Sclerorhynchus	*fanninensis*	Campanian	Texas	N. America
Sclerorhynchus	n. sp.	Cenomanian	Mississippi	N. America
Sclerorhynchus	n. sp.	Campanian	Peru	S. America
Sclerorhynchus	*palaeocenicus*	Paleocene (misident.)	Morocco	N. Africa
Sclerorhynchus	*pettersi*	Maastrichtian	Texas	N. America
Sclerorhynchus	*priscus*	Turonian-Coniacian	Texas	N. America
Sclerorhynchus	sp.	Campanian	Israel	Near East
Sclerorhynchus	sp.	Campanian	Mississippi	N. America
Sclerorhynchus	sp.	Senonian	Morocco	N. Africa
Sclerorhynchus	sp.	Campanian	Texas	N. America
Sclerorhynchus	sp.	Turonian-Coniacian	Texas	N. America
Sclerorhynchus	sp.	U. Cretaceous		Arabia
Sclerorhynchus?	sp.	Campanian?	Japan	Pcific
Sclerorhynchus?	sp.	Campanian-Maastricht.	New Zealand	Pacific
Sclerohynchidae	indet.	Campanian-Maastricht.	Peru	S. America
Sclerohynchidae?	indet.	U. Albian-L. Cenom.	England	Europe
Sclerorhynchidae?	indet.	Campanian	NW. Germany	Europe