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The Cretaceous Selachian Genus, *Ptychotrygon* JAEKEL 1894

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ABSTRACT

Ptychotrygon JAEKEL 1894 is a monotypic genus of selachians based upon isolated teeth (*Ptychodus triangularis* REUSS) from Upper Cretaceous rocks of Czechoslovakia. Citations do not extend the taxon beyond the general area and range of the original description.

We have found *Ptychotrygon* to be widespread in the Upper Cretaceous of Texas. This information and that from a few samples elsewhere demonstrate a minimal geographic distribution from Texas to Alabama toward the east and to South Dakota toward the north and a minimal temporal range from Late Cenomanian to latest Maestrichtian. In Texas specimens display properties of the type species and of two new species, which are described herein.

This material permits modification of the genus, emphasizing the external (labial) proboscoid extension of the crown and truncation of the internal (lingual) protuberance of the base and crown. This latter property serves to distinguish *Ptychotrygon* from the similar *Squatirhina* CASIER 1947, an orectolobid in which the internal protuberance is prominent; the former property distinguishes *Ptychotrygon* from *Hypolophus* MÜLLER and HENLE 1860, a dasyatid in which the crown is tabular.

Introduction

Ptychotrygon JAEKEL 1894 is a monotypic genus of selachians based upon isolated teeth (*Ptychodus triangularis* REUSS 1844, 1845) from the Kreideformation of Bohemia. It has been reported from Upper Cretaceous rocks in the environs of the Bohemian Massif only and would appear to be a provincial form.

However, we have found it to be a minor but ubiquitous element of fish faunas from the Gulf Series (Cenomanian-Maestrichtian) in northeast Texas. From a few samples of correlative rocks elsewhere, we have learned that it occurs throughout the Gulf Coastal Plain of the USA. H. Capetta, University of Montpellier (personal communication), has found the type and a new species in the Carlisle Shale (Turonian) of South Dakota, which is within the Western Interior Province of Cretaceous Rocks of the United States and Canada. Our material includes the type and two new species, which are described herein. In addition it provides new information on the genus, which is revised accordingly.

Because of their small size and low frequency in faunas, teeth of *Ptychotrygon* are rarely found without use of micropaleontologic methods in which rock samples are

disaggregated, sieved for concentrate, and picked of desired elements under microscopic observation. Even then it is advisable to take samples of at least 25 kg and to sample only glauconitic-phosphoritic rocks. Most of our several hundred specimens were recovered from the Bells Sandstone Member of the Eagle Ford Shale (McNULTY 1966; uppermost Turonian) or the lowermost Austin Chalk (McNULTY 1964; lowermost Coniacian) of northeast Texas. However, we have collected teeth from 37 localities which extend from the Rio Grande in westernmost Texas to Alabama on the east and to South Dakota on the north and which include 14 distinct glauconitic-phosphoritic horizons in the Gulf Series and equivalents. For this report 478 specimens were examined.

We are grateful to Messrs. Reed Hoover, Roy Pickerel, Ronald Ritchie, and Frank Schneider for aid in recovery of specimens. We are indebted to Dr. John Dismant, University of Texas for the Permian Basin, for the samples from the Aguja Formation, to Dr. Jiri Zidek, University of Oklahoma, for information on the destruction of E. A. REUSS's typic material, and to Dr. Emile Pessagno, Jr., University of Texas at Dallas, for access to the scanning electron microscope, which produced our illustrations of teeth.

Systematic Descriptions

Subclass Elasmobranchii

Order Batoidea

Family Dasyatidae

Genus *Ptychotrygon* JAEKEL 1894, revised

Type species. Ptychotrygon triangularis (REUSS) JAEKEL 1894, p. 133, textfig. 27 [= *Ptychodus triangularis* REUSS 1844, p. 218, 256; 1845, p. 2, Pl. II, Fig. 14–19]. Fixed by original designation and by monotypy. Gr. *ptychos*, fold; *trygon*, sting ray; presumably an allusion to the prominent corrugations on the crown and to the dasyatid (= trygonid) form of the base.

Description. Transversely elongate and tapering, typically bilaterally symmetrical teeth of approximately rhombic occlusal outline and generally batoid form; crown variably pyramidal, extended and somewhat overhanging at the exterior (= anterior, labial) angle, base columnar, restricted coronally, rhombic to hexagonal in basal outline and cleft basally by antero-posterior groove into which the pulp cavity opens widely; microstructure of crown dense and columnar in thick zone beneath enameloid layer, coarsely and dendroidally canaliculate (= osteodentine with branching pulpal canals of BERTIN 1958, p. 515, Fig. 320A) thence to the large irregular pulp cavity; microstructure of root coarsely and variously canaliculate.

Similar to *Squatirhina* CASIER 1947, from which it can be distinguished by its truncate and slightly concave instead of expanded and convex posterior angle of crown and its dasyatid instead of orectolobid base; similar to *Hypolophus* MÜLLER and HENLE 1860, from which it can be distinguished by its proboscoïd, pyramidal instead of tabular crown.

Distribution. Cenomanian through Maestrichtian, environs of Bohemian Massif, Europe; Texas, Arkansas, Alabama, Gulf Coastal Plain, and Western Interior, USA.

The range in absolute size is indicated by the variation in the greatest dimension (breadth) of the individual tooth from 0.5 to 5.0 mm. The type species, *P. triangularis* (REUSS), is prevailingly the largest; *P. agujaensis* n.sp. is the smallest species.

The relations of crown dimensions are approximated by the progression of $1\frac{1}{2} - 1 - 2 - 4$, representing the height of base, height of crown, length of crown, and breadth of crown.

From our material we recognize three species, which are distinguished from one another by properties of the crown, as illustrated schematically in Figure 1 and as stated below:

P. triangularis (REUSS) – crown with coarse, relatively distant, transverse corrugations;

P. hooveri n.sp. – crown with smooth faces and faint apical angles;

P. agujaensis n.sp. – crown with low and rounded, relatively crowded, transverse corrugations.

Judging from original description and illustration, *Raja texana* LERICHE (1942) is a ptychotrygonid, but neither kind of information permits satisfactory determination of crown properties, and its relations to other species of *Ptychotrygon* is indeterminate at present.

Ptychotrygon triangularis (REUSS), revised

Pl. I, Fig. 1–5, 16, 17

Ptychotrygon triangularis JAEKEL 1894, p. 136, Fig. 27a, b.

Ptychodus triangularis REUSS 1844, p. 218, 256; 1845, p. 2, Pl. II, Fig. 14–19; WOODWARD 1889, p. 152. *Acrodus triangularis* BRONN 1848, p. 9; GEINITZ 1850, p. 88; FRITSCH 1870, p. 222; 1878, p. 16, Fig. 38; 1889, p. 6, 10, 53, 67, Fig. 32; ZAHALKA 1899, PASMO IX, p. 18, 24, PASMO X, p. 30.

Neotype: *Ptychotrygon triangularis* REUSS; JAEKEL 1894, p. 134, Figures 27a, b; catalogue number 1864-XL-68, in Museum of Natural History of Vienna, from Planer Beds near Bilin, Czechoslovakia; neotype by designation here (see Remarks below).

Diagnosis. Ptychotrygonid teeth with covertly pyramidal crown, ornamented by three well separated, prominent, transverse corrugations, respectively, across the middle of the anterior face, along the junction of the anterior and posterior faces, and across the middle of the posterior face; also often bearing numerous, variously directed but smaller corrugations on the lower portions of the anterior face.

Distinguished from *P. agujaensis* n.sp. by the relative prominence, sharpness, and separation of major transverse corrugations, absence of smaller corrugations, and by higher and more elongate crown; from *P. hooveri* n.sp. by the presence of strong corrugations and more obscurely pyramidal crown.

Distribution. Temporal range from late Cenomanian through Maestrichtian; geographic range environs of Bohemian Massif, Europe; Texas, Arkansas, Alabama and South Dakota, USA.

This species occurs in the Littig Member of the Kincaid Formation of Texas. The Littig is the basal greensand of the Kincaid and is generally considered earliest Paleocene. But these beds contain reworked Cretaceous forms, of which *P. triangularis* may be one. Therefore, the temporal range of *P. triangularis* is here considered restricted to the Cretaceous Period.

In our samples this species occurs in marine rocks only and is more abundant in those of apparent outer neritic environment.

Dimensions. Specimens vary from 0.9 to 5.0 mm in the greatest dimension. Measurements of illustrated specimens (Pl. I) are given below (in millimeters).

Number	Height base	Height crown	Length crown	Breadth crown
1601	0.16	(broken)	2.40	4.80
1602	0.60	1.20	1.90	3.80
1603	0.50	1.00	1.80	3.00
1605	0.55	1.10	1.70	2.95
1620	0.62	1.30	2.25	—

Nature of material. 367 isolated teeth from 26 localities.

Depositories. The illustrated specimens, U.T.Ar. 1601–1605 and 1620, will be deposited in the University of Texas at Arlington Paleontological Collection. Additional specimens will be sent to the museums listed at the end of this paper.

Remarks. REUSS did not designate a holotype among his syntypes, and JAEKEL did not choose a lectotype, although the latter did figure two teeth from REUSS' type locality and indicated their depository as the "k. k. Naturhistorischen Hofmuseum in Wien" (*idem*, p. 134, Fig. 27a–d).

In 1967 Dr. Jirí Zidek, who was then at the National Museum in Prague, advised us (personal communication) that all of REUSS' typic materials had been lost during the civil war of 1956 in Budapest, to which they had been moved from Bilin. This situation raises the question of a neotype.

According to Article 75 of the International Code of Zoological Nomenclature (STOLL et al. 1964), loss of a holotype is not alone sufficient basis for designation of a neotype. However, Dr. Heinz KOLLMAN has advised us (personal communication, 1969) that JAEKEL's specimens are present in the collections of the Naturhistorisches Museum, Vienna, under the number 1864-XL-68. We have reported the foregoing facts to and solicited opinion from a number of paleoichthyologists (MCNULTY and SLAUGHTER 1970). Few replied, but all of them would prefer designation of a neotype.

Thus we here select JAEKEL's specimen that he illustrated by Figures 27a and 27b. The specimen of Figures 27c and 27d bears the same Museum number but is easily distinguished by its much longer and consequently more triangular crown (in occlusal view).

There is considerable variation in secondary corrugation and in length to breadth ratio of crown, as REUSS' illustrations (1845, Pl. II, Fig. 14–19) show. High l/b ratios produce forms of conspicuously triangular occlusal outline (REUSS 1845, P. II, Fig. 16, 17), which may have provoked the trivial nomen. Such forms are a small percentage of our material.

Ptychotrygon hooveri n.sp.

Pl. I, Fig. 6–10

Etymology. Patronym in dedication to Mr. Reed Hoover, amateur paleontologist, Dallas, Texas, for his long, unselfish, and capable work in paleontology of rocks in northeast Texas.

Holotype, horizon and locality. – *Ptychotrygon hooveri* n.sp., The University of Texas at Arlington Paleontological Collection, 1606, paratype 1607–1610; Bells Sandstone Member (Late Turonian; McNULTY 1966, p. 375; KEROHER 1970, p. 57), Eagle Ford Formation; northwest corner of Marsh Lane and Interstate Highway 635, Dallas, Texas, USA; road cut on north side of I-635, exposing two 8-cm layers of gray phosphoritic, quartzose sandstone, situated 30 cm apart in the upper five feet of dark, olive gray shale.

Diagnosis. Ptychotrygonid teeth, crown pyramidal, smooth, with faint apical angles.

Differs from both *P. triangularis* (REUSS) and *P. agujaensis* n.sp. in its lack of transverse corrugations.

Distribution. Temporal range from late Cenomanian to Coniacian; geographic range, northeast Texas.

This species is most common in quartz sandstones of inner neritic aspect.

Dimensions. Specimens vary from 0.75 to 3.2 mm in the greatest dimension of the individual. Measurements of the holotype and the paratypes are given below (in millimeters).

Number	Height base	Height crown	Length crown	Breadth crown
1606	0.30	0.65	1.15	2.00
1607	0.25	0.60	1.20	1.95
1608	0.30	0.70	1.20	1.85
1609	0.30	0.60	0.95	1.90
1610	0.30	0.60	1.10	2.30

Nature of material. Fifty seven isolated teeth from ten localities in northeast Texas.

Depositories. The holotype and paratypes will be deposited in the University of Texas at Arlington Paleontological Collection with accession numbers of 1606 for the holotype and 1607–1610 for the paratypes. Additional specimens will be sent to the museums listed at the end of this paper.

Remarks. Irregular corrugations of low relief may occur on the anterior faces, particularly on the lower portions of the crown. Morphologically this species is gradation into *P. triangularis*, and specimens of intermediate form are common in samples from the oldest horizon (Cenomanian) of our collections.

Ptychotrygon agujaensis n.sp.

Pl. I, Fig. 11–15

Etymology. Geographic substantive, derived from the Sierra Aguja, Brewster County, Texas, around which strata of the Aguja Formation crop out and from which they take their name.

Holotype, horizon and locality. The University of Texas at Arlington Paleontological Collection, 1611, paratypes 1612–1616; Aguja Formation (Campanian, ADKINS 1933, p. 505; KEROHER 1966, p. 29); west side of arroya which is traversed by old Terlingua Road at a point about two miles south of its intersection with State Highway 118; approximately 70 miles south of Alpine, Texas; yellowish brown, fine to coarse grained, calcareous, phosphoritic sandstone at top of hill.

Diagnosis. Ptychotrygonid teeth, crown low and rounded, with closely spaced, low and rounded, transverse corrugations.

Distinguished from *P. triangularis* (REUSS) by the larger number, closer spacing, and lower, more rounded form of transverse corrugations. Also the crown is usually lower than in any other species.

Distribution. Known only from type locality.

Dimensions. Specimens measure from 0.50 to 2.5 mm in the greatest dimension of the individual. Measurements of the holotype and paratype are given below (in millimeters).

Number	Height base	Height crown	Length crown	Breadth crown
1611	0.20	0.45	0.80	1.80
1612	0.40	(broken)	1.00	2.40
1613	0.30	0.60	1.11	2.00
1615	0.25	0.50	0.85	1.85
1616	0.30	0.60	1.00	2.25

Nature of material. Fifty-four specimens from the type locality.

Depositories. The holotype, U.T.Ar. 1611, and the paratypes U.T.Ar. 1612–1613, 1615–1616, will be deposited in the University of Texas at Arlington Paleontological Collection. Additional specimens will be sent to the museums listed at the end of this paper.

Remarks. The majority of specimens of *P. agujaensis* n.sp. are distinctly appressed in crown and root, particularly the latter which is often so short that it is fragile and consequently broken.

Some specimens are longer and higher in crown, approaching *P. triangularis* (REUSS) and suggesting derivation therefrom.

Ptychotrygon texana (LERICHE)

Raja texana LERICH 1942, p. 12, 13, Pl. I, Fig. 5.

Remarks. LERICHE's illustrations show clearly the *Ptychotrygon* crown, including the truncate posterior with its oval, slightly concave surface on the posterior angle.

Both description and illustration portray a smooth-surfaced form which resembles *P. hooveri* n.sp. except for the angularity of apical angles of the latter form. *P. texana* is based upon a single specimen from a road cut (now deeply weathered and grass covered) in the Littig Member (Early Danian) of the Kincaid Formation of the Midway Group (Paleocene). We have sampled the Littig a few miles to the south where the type locality is situated and recovered *P. triangularis* but nothing that resembled *P. texana*.

Thus the holotype is unavailable and we have been unable to recover additional material, leaving only the original description for evaluation of this species. As noted above, the original description does not give adequate specific information, and the status of this species is presently beyond resolution.

Systematic relations

Both crown and base of *Ptychotrygon* teeth have systematic implications. The former resembles the crown of galeoids, such as *Squatina* DUMERIL 1806, *Ginglymostoma* MÜLLER and HENLE 1837, and *Squatirhina* CASIER 1947, particularly in the presence of a proboscoïd extension at the anterior angle. The latter resembles dasyatid batoids, especially *Hypolophus* MÜLLER and HENLE 1860. All of these have a record that extends from the present back into Early Cretaceous or Late Jurassic time, except *Ptychotrygon*.

The contradictory implications of ptychotrygonid crown and base suggest an intermediate position in the galeoid-batoid succession. CASIER (1947) has proposed that *Squatina*, *Ginglymostoma* and *Squatirhina* form a morphologic sequence extending from the galeoid form toward the batoid, and *Ptychotrygon* would fit well into such a succession, representing a form which has lost its expansion of the internal, posterior angle (protuberance interne of CASIER 1947) to form the hypolophid (Dasyatidae) base and posteriorly truncate, squatirhinid (Orectolobidae) crown (Fig. 2).

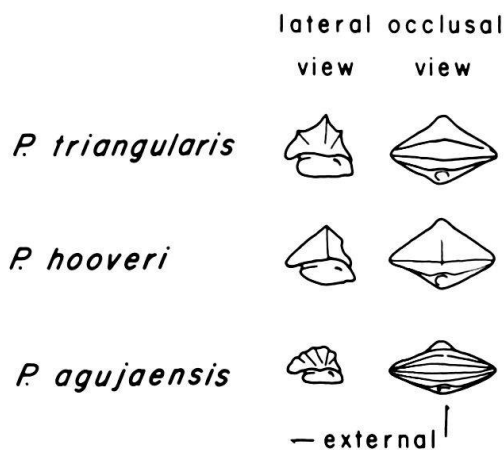


Fig. 1. Schematic illustration of crown properties that distinguish species of *Ptychotrygon*

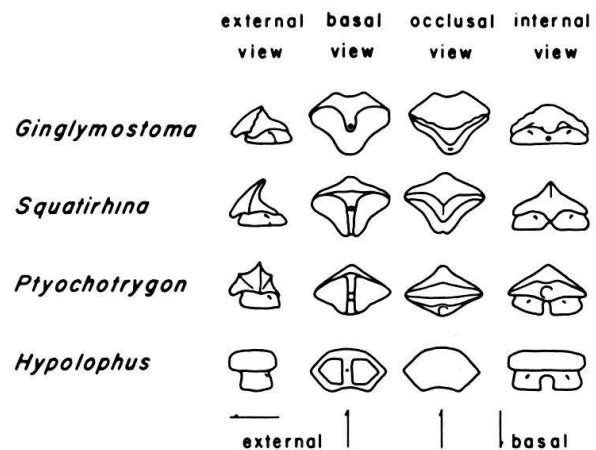


Fig. 2. Schematic illustration of genera with properties of teeth similar to *Ptychotrygon*.

Such a sequence appears to by-pass the rhinobatid and rajiid batoids, raising the question of polyphyletic transition from galeoid to batoid form. And the sequence is apparently contradictory to the implication of hypolophid range, which extends beyond that of ptychotrygonid into the Aptian and makes hypolophids improbable successors of the subsequently appearing (Cenomanian) ptychotrygonids.

To be noted also is the concurrence of ganopristid rostral teeth in the Cenomanian of northeast Texas, for which the oral dentition remains to be demonstrated (McNULTY and SLAUGHTER 1962, 1964). On the bases of form and association, *Ptychotrygon* teeth are the most suitable and appealing possibility for ganopristid oral dentition. If they prove to be such, their placement in current classification would be settled at ordinal (Batoidea) and familial (Pristidae) levels.

At present the systematic position of *Ptychotrygon* is beyond determination at even the ordinal level; consequently, the classification employed above is practicable but questionable.

Depositories

- Australia*: National Museum of Victoria, Melbourne
Austria: Natural History Museum, Vienna
Germany: Geological-Paleontological Institute, Tübingen
Belgium: Royal Institute of Natural Science, Brussels
Czechoslovakia: National Museum, Prague
Africa: Paleontological Institute, Witwatersrand University, Johannesburg
Canada: National Museum, Ottawa
England: British Museum (Natural History), London
France: National Museum of Natural History
India: Paleontological Division, Geological Survey, Calcutta
Japan: Department of Paleontology, National Science Museum, Tokyo
Russia: Paleontological Institute, Academy of Sciences, Moscow
Sweden: Natural History Museum, Stockholm
USA:
 California: Los Angeles County Museum of Natural History, Los Angeles
 District of Columbia: US National Museum, Washington
 Illinois: Field Museum of Natural History, Chicago
 New York: American Museum of Natural History, New York
 Pennsylvania: Carnegie Museum, Pittsburgh
 Shuler Museum of Paleontology, Southern Methodist University, Dallas, Tex.
 Texas: Texas Memorial Museum, Austin

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Plate I

- Fig. 1–5 *Ptychotrygon triangularis* (REUSS): 1 U. T. Ar. 1603, 10×, lateral view. 2 U. T. Ar. 1602, 10×, anterior view. 3 U. T. Ar. 1605, 10×, occlusal view. 4 U. T. Ar. 1620, 10×, longitudinal section. 5 U. T. Ar. 1601, 10×, basal view.
- Fig. 6–10 *Ptychotrygon hooveri* n. sp.: 6 U. T. Ar. 1608, 13×, anterior view. 7 U. T. Ar. 1610, 13×, occlusal view. 8 U. T. Ar. 1606*, 15×, basal view. 9 U. T. Ar. 1609, 15×, posterior view. 10 U. T. Ar. 1607, 10×, lateral view.
- Fig. 11–15 *Ptychotrygon agujaensis* n. sp.: 11 U. T. Ar. 1616, 15×, occlusal view. 12 U. T. Ar. 1613, 15×, anterior view. 13 U. T. Ar. 1612, 15×, lateral view. 14 U. T. Ar. 1615, 10×, oblique postero-occlusal view. 15 U. T. Ar. 1611*, 15×, basal view.
- Fig. 16–17 *Ptychotrygon triangularis* (REUSS), 10×, occlusal views; illustrating degree of crown ornamentation intermediate between *P. triangularis* and *P. hooveri*.

* Holotype; others of species are paratypes.

