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Sapperichthys gen. nov., a new gonorynchid from the Cenomanian of Chiapas, Mexico

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Abstract

Sapperichthys gen. nov. is described herein based on new Cenomanian specimens from the Sierra Madre Formation, Chiapas, Mexico. This new gonorynchid exhibits several diagnostic characters of the Gonorynchiformes such as the absence of orbitosphenoid and basisphenoid, the anterior neural arches expanded in the lateral plane, and the presence of three sets of intermuscular bones; and of the Gonorynchidae such as the elongate and narrow frontal bone except in postorbital region and the presence of two patches of conical teeth. It is diagnosed as a valid taxon and a basal gonorynchid on the basis of characters such as the presence of a rounded opercle with a spiny posterior border; a smooth subopercle; a vertical oriented and triangular hyomandibular head; a wide metapterygoid; a V-shaped dentary, loosely articulated with the anguloarticular; medially expanded supraneurals, not in contact with each other, and loosely articulated with the neural arches; about 40 vertebrae; and 11 dorsal fin rays. This new taxon is the oldest record for the Gonorynchiformes in North and Central America, suggesting an origin of the Gonorynchidae probably related to the opening of the Mediterranean/Caribbean Tethys.

Introduction

The Gonorynchiformes (sensu ROSEN & GREENWOOD 1970), are composed of three families: Chanidae, including the extant genus *Chanos* and fossils from Europe, Africa, and South America (POYATO-ARIZA 1996); Gonorynchidae, including the extant *Gonorynchus* and fossils from North America, Africa, and Europe (GRANDE & POYATO-ARIZA 1999, GRANDE & GRANDE 2008a); and Kneriidae, with fossil (see DAVIS et al. this volume) and extant forms from African freshwater drainages.

The knowledge of Cretaceous gonorynchiforms in Mexico began with APPLEGATE (1996) reporting the occurrence of a large gonorynchiform fish from the Albian Tlayúa Quarry (Puebla State), in Central Mexico. In 2008, ALVARADO-ORTEGA & NÚÑEZ-UTRILLA (2008) reported the occurrence of additional material from the Tlayúa Quarry. ALVARADO-ORTEGA et al. (2009) illustrated and preliminarily described two specimens belonging to this order from the Cenomanian Sierra Madre Formation strata at El Chango Quarry (Chiapas State). In addition, two gonorynchiform specimens were collected by J.A.O. in 2009 in Paleocene outcrops near Palenque (Chiapas State). Until APPLEGATE (1996), the fossil record of the gonorynchiforms in North and Central America was restricted to a single genus, *Notogoneus* (COPE 1885), best known from the Eocene Fossil Butte Member of the Green River Formation, southwestern Wyoming, USA (GRANDE & GRANDE 2008a).

The main objective of the present paper is to describe a new gonorynchiform from the lithographic limestones of Sierra Madre Formation, Chiapas, Mexico, originally reported by ALVARADO-ORTEGA et al. (2009). This description is based on two specimens (IHNFG2986 and IHNFG8943), collected on the outcrops of El Chango Quarry, Chiapas State, currently housed in the collection of the Museo de Paleontología Eliseo Palacios Aguilera, in Chiapas, Mexico, and registered under the acronym IHNFG. The holotype (IHNFG2986) is a partially preserved specimen, exposed on its right side and missing the caudal endoskeleton due to breakage posterior to the dorsal and pelvic fins.

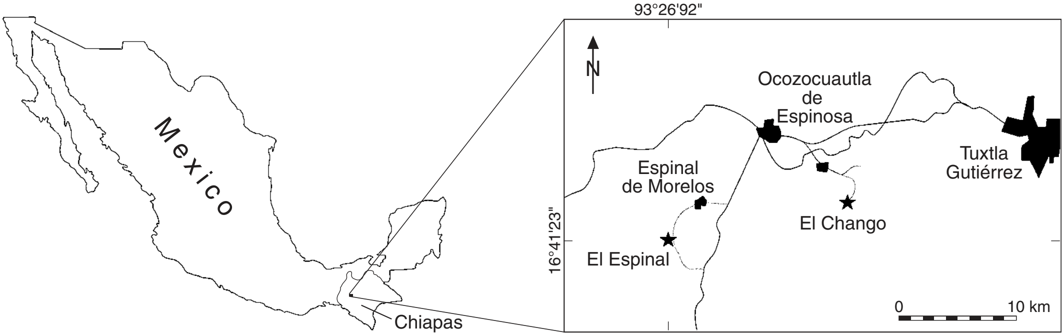

Fig. 1.
Map of the region of Ocozocoautla de Espinosa, Chiapas, Southern Mexico. The star indicates the El Chango Quarry and the dark gray areas show the Sierra Madre Formation outcrops.

Geological Setting and Age

The specimens were collected from the outcrops of El Chango quarry (N 16°34'14.9" / W 93°16'12.7"), located at the southern region of Ocozocoautla de Espinosa (Fig. 1) which is formed by monotonous layers of dolomitic carbonates that had been accumulated within an estuary or salty lagoon with ephemeral fresh-water contact (VEGA et al. 2006, 2007). Fossils from this locality mainly include fishes, plants, mollusks, crustaceans, and insects (ALVARADO-ORTEGA et al. 2009).

The strata exposed in El Chango have been assigned to the Sierra Madre Formation under the criteria of their geographic distribution within the Ocozocoautla area. However, as pointed by ALVARADO-ORTEGA et al. (2009) and ALVARADO-ORTEGA & THAN-MARCHESE (2012), the total thickness, the lateral boundaries, and the relation of the strata exposed in the El Chango quarry and the lithological units of the Sierra Madre Formation, as described by STEELE (1986) and WAITE (1986), still remain unknown.

BÖSE (1905) described the Cretaceous platform carbonate series that includes dolomites and limestones bearing flints exposed along Sierra Madre, central Chiapas, as “Cretaceous limestones with rudists”. Later, these strata were recognized under different names; VER WIEBE (1925) suggested the San Cristobal Formation and NUTALL (1929, in SALAS, 1949) gave them the name of the Sierra Madre Formation which is so far the only one in use. The Sierra Madre limestones were divided in two sequences by SALAS (1949); a non-fossiliferous Albian-Cenomanian unit of sugary aspect limestones and a Turonian unit of limestones with flints and rudists. This observation was formalized by GONZÁLEZ (1963), who recognized these units as the Cantelhá and the Jolpabuchil members, respectively. Soon, petroleum exploration brought the discovery of microfossils and the opportunity to identify accurate ages. GUTIÉRREZ-GIL (1956), on the basis of the presence of the rudists *Radiolites* sp., *Caprina* sp., and *Toucasia* sp., suggested a Lower Cretaceous age for the base of the Sierra Madre Formation. Later, SÁNCHEZ-MONTES DE OCA (1969), based on the presence of the foraminiferans *Dicyclina schlumbergeri* and *Nummoloculina heimi*, suggested a late Albian to Cenomanian age. Finally, the latter author described the Turonian-Maastrichthian Jolpabuchil strata as a formation and recognized two members: the Albian Cantelhá Member and the late Albian-Cenomanian Cintalapa Member. Currently, this nomenclature of the Sierra Madre limestones continues in use, but in the work of Mexico’s petroleum geologists, this unit has been elevated to Group rank and its members are frequently referred as formations (MANDUJANO-VELASQUEZ & VAZQUEZ-MENESES, 1996).

Despite all these previous publications, STEELE (1986) and WAITE (1986) treated the limestones of the Sierra Madre Formation from Chiapas as a single formation, in which they recognized a sequence with litho and biostratigraphic units that were only given sequential numbers.

STEELE (1986), based on the presence of the foraminifers *Nummoloculina heimi*, *Simplorbitolina* sp., and *Coskinolinoides* sp., assigned a late Aptian to Santonian age for the entire sequence of the Sierra Madre Formation. Additionally they suggested a ?Neocomian/early Albian age for the basal dolomitic strata, which correspond to El Chango and the nearby El Espinal quarries. MICHAUD (1987) noted the presence of the foraminifers *Praechrysalidina* sp. cf. *P. infracretacea*, and suggested a late Aptian/early Albian age for this unit.

OVALLES-DAMIÁN & ALVARADO-ORTEGA (2002) studied a paraclupeid fish from the El Espinal quarry, recognizing it as closely related to *Paraclupea* SUN, 1956, from Aptian freshwater deposits of China, and suggesting the same age for this locality. Later, VEGA et al. (2006, 2007) studied the invertebrate fauna from El Espinal and El Chango quarries, concluding that an Aptian age is valid for both localities. Recently, ALVARADO-ORTEGA et al. (2009), THAN-MARCHESE & ALVARADO-ORTEGA (2010), and ALVARADO-ORTEGA & THAN-MARCHESE (2012, 2013), based on the fish assemblage, suggested a Cenomanian age for the locality based on the taxonomic similarity between the Mexican and the Middle Eastern/Eastern European Cenomanian fish assemblages.

The sediments from the El Chango quarry correspond to the 700–1600 meter-thick sequence of the Cenomanian Cintalapa strata (J. A.-O. pers. obs. 2010) of the Sierra Madre Formation, which consist of cream-colored dolomite, biomicrites, and dolomitized micrites with some white chert lenses (ÁLVAREZ-MENA 1975). Therefore, we consider the dolomitic limestone strata of the El Chango quarry, from where the specimens were collected, as Cenomanian in age.

Systematic Palaeontology

Superorder Ostariophysi sensu ROSEN & GREENWOOD, 1970
Order Gonorynchiformes sensu ROSEN & GREENWOOD, 1970
Family Gonorynchidae sensu GRANDE & POYATO-ARIZA, 1999

Sapperichthys, gen. nov.

Diagnosis (based on a unique combination of characters)**.** Medium sized gonorynchid fish differing from the other members of the family in presenting: a wide metapterygoid; a V-shaped dentary, loosely articulated with the anguloarticular; a rounded opercle with a spiny posterior border; a smooth, broad subopercle medially expanded; supraneurals, not in contact with each other, and loosely articulated with the neural arches; about 40 vertebrae; 11 dorsal fin rays.

Type-species. *Sapperichthys chiapanensis*, sp. nov.

Etymology. The generic name honors Karl Theodor SAPPER (1866–1945), a German naturalist and surveyor, and pioneer in the description of the geology and paleontology of Chiapas, Mexico.

Sapperichthys chiapanensis, sp. nov.

Holotype: IHNFG2986, partially preserved specimen in its right side. The posterior part of body just posterior to the dorsal fin is lacking (Fig. 2).

Referred specimens: IHNFG2993, partially preserved specimen in ventral view. The posterior caudal region, including the caudal endoskeleton, is missing (Fig. 3).

Horizon and locality: Cenomanian limestones of El Chango Quarry, Sierra Madre Formation, Chiapas, Mexico (see above for details).

Diagnosis: As for genus (monotypic).

Etymology. The specific epithet refers to the Mexican State of Chiapas, where the fossils representative of this new species was collected.

Description and comparisons

Sapperichthys chiapanensis is a medium-sized gonorynchiform about 15 to 20 cm long and known from three partially preserved specimens, all three lacking the caudal endoskeleton. The holotype is preserved as far posteriorly as the 27th vertebra (Fig. 2). Specimen IHNFG2993 (in part and counter-part) is preserved in ventral view from the snout to the 40th vertebra. Unlike most other gonorynchids, except for the Middle-Eastern Cretaceous genera *Ramallichthys*, *Hakeliosomus*, and *Charitosomus*, which exhibit 42–43 vertebrae, *Sapperichthys chiapanensis* has a reduced number of vertebrae, thus differing from *Notogoneus*, which has 50–52 vertebrae, and the extant genus *Gonorynchus*, which has 54–66 total vertebrae.

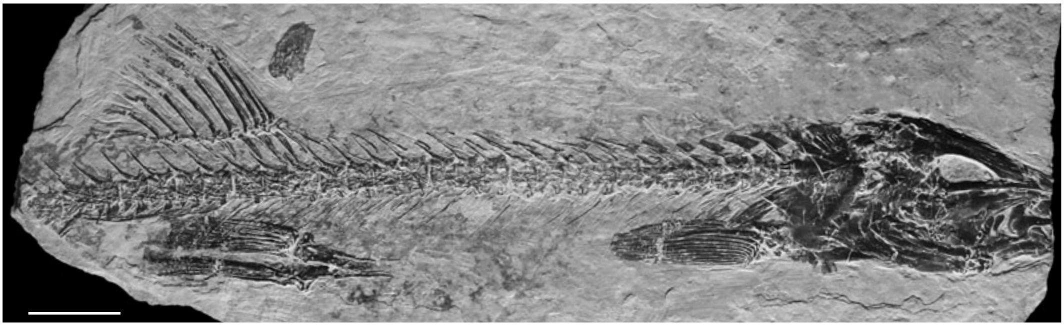

Fig. 2.
Sapperichthys chiapanensis, gen. et sp. nov., holotype (IHNFG2986). Scale bar = 1 cm.

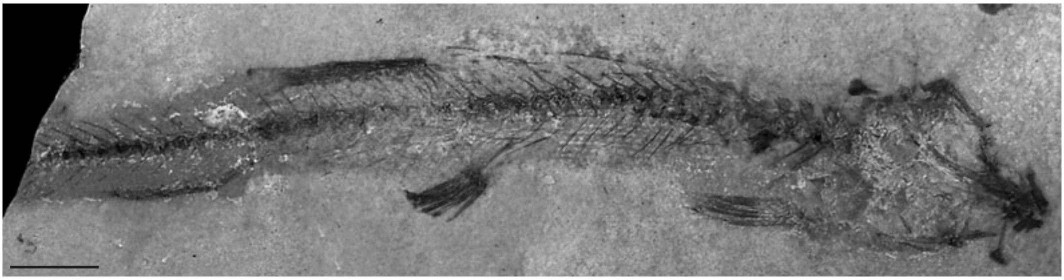

Fig. 3.
Sapperichthys chiapanensis, gen. et sp. nov. (IHNFG2993). Scale bar = 1 cm.

Additionally, *Sapperichthys* has 11 dorsal fin rays, differing from *Notogoneus* with its 13–15 dorsal fin rays, and from *Ramallichthys* and *Hakeliosomus* with 13 and 10 dorsal fin rays, respectively. Table 1 summarizes the meristic data of the fossil and Recent Gonorynchidae including *Sapperichthys chiapanensis*.

The anatomical terminology of skull-roof bones adopted herein follows the traditional actinopterygian terms.

Skull roof and braincase. The anterior part of the cranial roof of the right side, as shown by specimen IHNFG 2986, is formed by a relatively wide frontal bone (Fig. 4) compared to that of other gonorynchids,

Table 1. Meristic data from fossil and recent gonorynchids with the inclusion of *Sapperichthys chiapanensis*. Adapted from GRANDE (1999) and GRANDE & GRANDE (2008b).

	Total centra	Postdorsal centra	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays
Ramallichthys orientalis	42	17	13	7	14–15	8
Judeichthys haasi	?	17	?	≥6	14	8
Hakeliosomus hakelensis	42–43	17	13	8	14–15	8
Charitosomus major	58–59	20	10	10	8	9
Charitosomus lineolatus	48+51–52	21–22	11	8	8	8–9
Charitosomus spinosus	42	20	12	7	9	9
Notogoneus osculus	50–52	12–15	13–15	8–10	9–10	8–9
Gonorynchus greyi	59–61	?	10–11	7–8	10–11	9
Gonorynchus gonorynchus	62–63	?	11–12	8–9	11	9
Gonorynchus abbreviatus	54–55	?	10	8	10	8
Sapperichthys chiapanensis	?40	?17	11	9	11	8

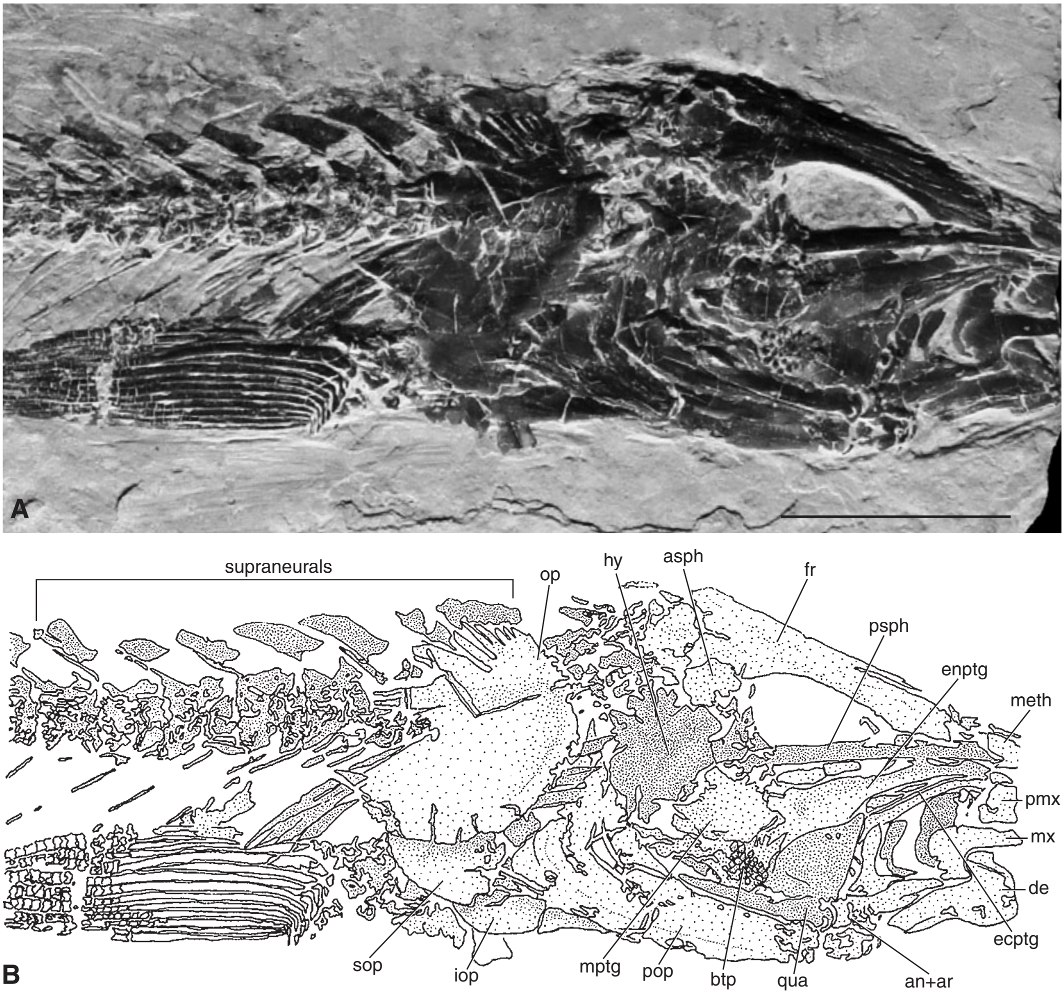

Fig. 4.
Sapperichthys chiapanensis, gen. et sp. nov. holotype (IHNFG2986). **A,** skull and pectoral region. **B,** anatomical interpretation. Scale bar = 1 cm. Abbreviations: **an+ar,** anguloarticular; **asph,** autosphenotic; **btp,** basibranchial toothplate; **de**, dentary; **ecptg**, ectopterygoid; **enptg**, entopterygoid; **etp**, entopterygoid toothplate; **fr**, frontal bone; **hy**, hyomandibula; **io**, infraorbital bone; **iop**, interopercle; **meth**, mesethmoid; **mptg**, metapterygoid; **mx**, maxilla; **op**, opercle; **pmx**, premaxilla; **pop**, preopercle; **psph**, parasphenoid; **qua**, quadrate; **rar**, retroarticular; **sop**, subopercle.

narrower dorsal to the orbits, and widening near the lateral ethmoid articulation. Anteriorly, the median mesethmoid is partially preserved, apparently extending beyond the anterior end of the vomer (Fig. 4). The orbitosphenoid and basisphenoid are absent.

The braincase is poorly preserved, except for the orbital region of the parasphenoid. In this region, the parasphenoid is robust and edentulous (Fig. 4). Near the otic region, the parasphenoid broadens as it forms the floor of the posterior myodome and contacts the prootic. A small and blade-like vomer is visible anteriorly (Fig. 4).

Dermal cheek bones. The preopercle is unornamented and exhibits a short vertical limb, and an elongated horizontal limb twice the length of the vertical limb. A small posterior expansion is present at the angle between the horizontal and vertical limbs (Fig. 4). The preopercular sensory canal runs near the anterior margin of the bone and is continuous, ventrally, with the mandibular sensory canal, which runs along the ventral border of the dentary. Two small, rectangular infraorbitals are displaced and located near the ventral margin of the parasphenoid in the orbital region.

Opercular series and branchiostegals. Differing from that of all other gonorynchids, the opercle is large, rounded, and located at about one third of the head length. Its posterior border exhibits a series of spines similar to those found in *Charitopsis spinosus* GAYET, 1993b (Fig. 4). Except for *Charitopsis* and the new genus *Sapperichthys*, all other gonorynchids have an opercle with a smooth posterior border; however, in *Charitopsis* the opercle is triangular, thus differing from the rounded opercle presented by *Sapperichthys*.

The subopercle and interopercle (Fig. 4) are partially covered by the ventral border of the opercle and preopercle, respectively. The subopercle exhibits a uniformly rounded posterior border without the diagnostic clefts present in the genus *Notogoneus*. The interopercle is triangular, smooth, and with a rounded posterior border and an anterior apex that is partially covered by the horizontal limb of the preopercle. No branchiostegals are visible.

Jaws. The upper jaw consists of a maxilla with an angle of 90° between its horizontal anterior articular process and its wide, vertically oriented posterior region (Fig. 4). The small premaxilla is partially visible in specimen IHNFG 2993 and resembles that of *Notogoneus*. The lower jaw includes a typical V-shaped dentary (Fig. 4) with an elongated and somewhat tapered posterior end, which loosely articulates with the anguloarticular. The anterior region of the dentary is wide, vertically oriented, and expanded. The anguloarticular is subtriangular with a long and narrow anterior process which articulates with the dentary, and a high dorsal process (Fig. 4). The inferior limb of the retroarticular process is not elongated and does not encapsulate the ventral region of the quadrate head. The retroarticular (Fig. 4) is only partially preserved as a small bone, located ventroposterior to the anguloarticular, and not participating in the quadrate-mandible articulation. The quadrate-mandible articulation is located at the level of the orbit.

Suspensorium, palate and gill arches. Of the right hyomandibular bone, only the double articular head is visible, with its anterior and posterior articular facets, which articulate with the autosphenotic and dermopterotic, respectively (Fig. 4). The hyomandibular head of *Sapperichthys* is vertical and triangular and resembles that in the Chanidae and Kneriidae, which exhibit a large angle formed by the alignment of the articular processes and the horizontal body axis. It differs from that of *Notogoneus* and *Gonorynchus,* which present an almost horizontal alignment of this articulation (see BRITZ & MORITZ 2007). The quadrate is broad and triangular, with the typical, long posteroventral process (Fig. 4). A symplectic is visible as a small rod, medial to the posteroventral process of the quadrate (Fig. 4). Unlike *Notogoneus* and *Gonorynchus,* which have a small, blade-like metapterygoid, the metapterygoid of *Sapperichthys* is broad and trapezoidal, similar to that found in chanids and the Middle Eastern gonorynchids *Ramallichthys orientalis* GAYET, 1982, and *Judeichthys haasi* GAYET, 1985. It is bordered anteriorly by the triangular endopterygoid and laterally by the ectopterygoid (Fig. 4).

Two toothplates were observed, both exhibiting small conical teeth. The endopterygoid toothplate is partially preserved under the ascending process of the parasphenoid (Fig. 4), with only a few teeth preserved. The basibranchial toothplate is well preserved near the posterior border of the quadrate (Fig. 4).

Vertebral column. We counted 40 vertebrae, 29 abdominal and 11 caudal, in specimen IHNFG2993, which is broken just anterior to the caudal endoskeleton. All the supraneurals are rectangular and loosely articulated with the apices of neural arches. These supraneurals and neural arches are medially expanded but not in contact with each other, becoming smaller posteriorly (Fig. 4), and resembling those of *Notogoneus* and *Gonorynchus*. The Middle-Eastern gonorynchids such as *Judeichthys* and *Ramallichthys* have large, expanded supraneurals in close contact with each other. Three sets of intermuscular bones are present but not satisfactorily preserved. The observed intermusculars resemble those found in *Gonorynchus* with forked epineurals, and simple epicentrals and epipleurals.

Pectoral and pelvic girdles and fins. The pectoral girdle is not well preserved. The anteroventral apex of the cleithrum is visible, under the ventral end of the subopercle. Posteriorly, four radials are visible articulating with eleven pectoral rays. The shape of the pectoral fin is somewhat triangular. The pectoral fin rays are segmented and branched, except for the first ray.

The pelvic bones are triangular with an anteriorly directed apex flanked by a narrow and robust ridge laterally (Fig. 6). The pelvic bones articulate with each other medially. No radials were observed. The pelvic

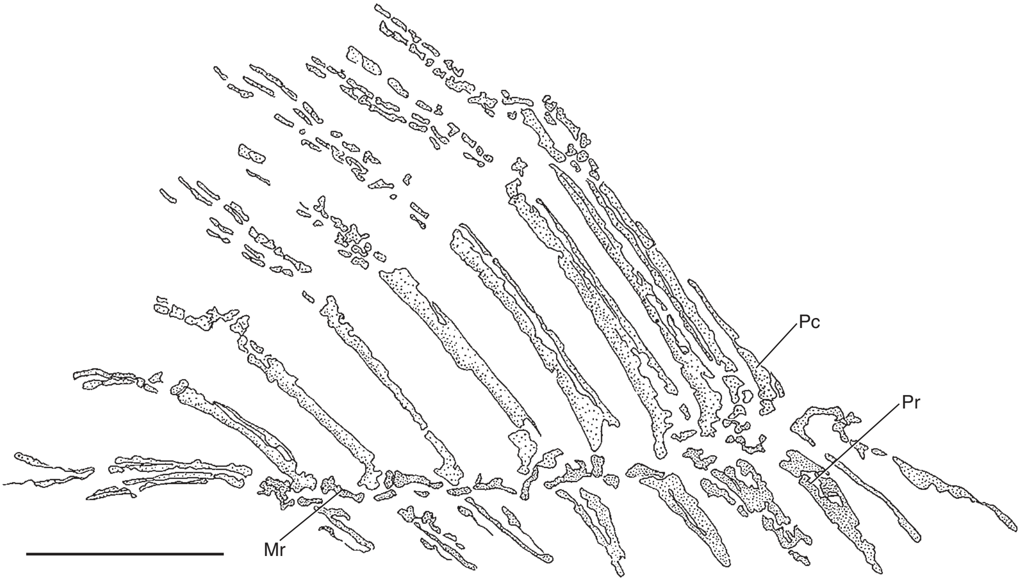

Fig. 5.
Sapperichthys chiapanensis, gen. et sp. nov., holotype (IHNFG2986). Dorsal fin. Scale bar = 1 cm. Abbreviations: **mr**, middle radial; **pc**, procurrent ray; **pr**, proximal radial.

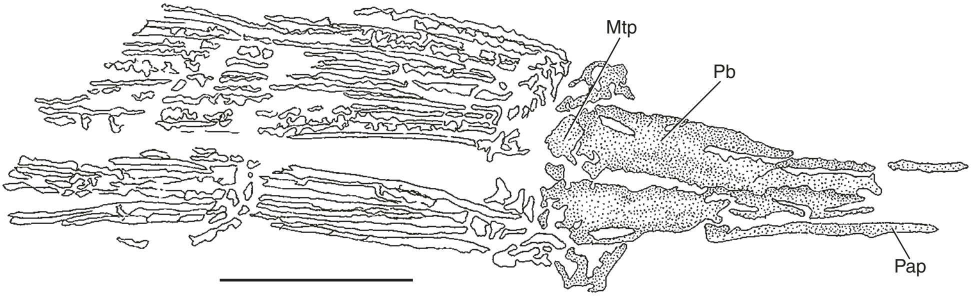

Fig. 6.
Sapperichthys chiapanensis, gen. et sp. nov., holotype (IHNFG2986). Pelvic fin and girdle. Scale bar = 1 cm. Abbreviations: **mtp**, metapterygium; **pap**, pelvic anterior process; **pb**, pelvic bone or basipterygium.

fins are rectangular and originate beneath the 23rd vertebra. Eight fin rays are visible in each fin, all except the first one branched and segmented.

Dorsal and anal fins. The dorsal fin is trapezoidal and originates above the 23rd vertebra. It is composed of eleven fin rays, ten segmented and branched principal rays, the last one double, and one small procurrent ray (Fig. 5). The dorsal fin rays decrease in length posteriorly and are supported by nine pterygiophores. The first pterygiophore is bifurcated.

The anal fin is poorly preserved in the only specimen in which it is preserved, IHNFG2993. It originates under the 33rd vertebra and is composed of nine anal fin rays. The fin shape could not be determined.

Scales. The scales are not satisfactorily preserved. No spines projected from the posterior margin were observed. The head is devoid of scales in both specimens as it is in all other gonorynchids, except for *Notogoneus* and *Gonorynchus*.

Phylogenetic Analysis

The most recent study concerning the phylogenetic relationships of the Gonorynchidae is the revision of GRANDE & GRANDE (2008b), which reevaluated the validity of the genera *Notogoneus*, *Ramallichthys*, *Judeichthys*, and *Hakeliosomus*, considering the last two as a synonym of *Ramallichthys orientalis*, and discussed the relationships within the Gonorynchidae. Two years later, the work of POYATO-ARIZA et al. (2010) corroborated the relationships of the basal gonorynchids as proposed by GRANDE & GRANDE (2008b).

The phylogenetic relationships of *Sapperichthys chiapanensis* within the Gonorynchidae were evaluated by two analyses, using cladistic methodology with both ACCTRAN and DELTRAN optimizations. We constructed a data matrix based on the characters proposed by POYATO-ARIZA et al. (2010) and followed the same analyses done by the authors, excluding the taxa considered as problematic (i. e., *Apullichthys*, *Lecceichthys*, *Halecopsis*, *Erfoudichthys*, and *Sorbininardus*), and treating as ordered the characters 3, 8, 13, 15, 33, 57, 77, 78, 82, 95, 97, 99, 100, and 102. The character states for *Sapperichthys chiapanensis* and a list of characters and their states, as proposed by POYATO-ARIZA et al. (2010), are present in the Appendix. For further discussion about the morphological characters, see POYATO-ARIZA et al. (2010).

The results of the analysis, running a heuristic search on PAUP 4b10 (SWOFFORD 1999) resulted in eighty-four most parsimonious trees with 233 steps (CI = 0.687, HI = 0.313, RI = 0.822, and RC = 0.564) (Fig. 7).

The strict consensus of the obtained topologies displays a total of fifteen components. We will discuss the relationships of *Sapperichthys* within component 7, the Gonorynchoidei.

The Gonorynchoidei (Fig. 7, Node 7) are diagnosed by 15 characters, 8 autapomorphic, and this result mainly agrees with POYATO-ARIZA et al. (2010), except for character 78 (contact between the anterior neural arches), present in the results of POYATO-ARIZA et al. (2010) for ACCTRAN optimization and absent in ours. Character 78 presents state 0 (no contact with adjoining arches) for *Sapperichthys* and *Notogoneus*, state 1 (abutting adjoining arches medially, without overlap) for *Gonorynchus* and the Kneriidae, and state 2 (overlapping contact with adjoining arches medially) as autapomorphic for the Middle Eastern gonorynchids (i. e., *Charitosomus*, *Charitopsis*, *Judeichthys*, *Hakeliosomus*, and *Ramallichthys*).

The Gonorynchidae (Fig. 7, Node 8) are diagnosed by 10 characters, 6 autapomorphic. With ACCTRAN optimization our result differs from that of POYATO-ARIZA et al. (2010) in the optimization of characters 26 (maxillary process for the palatine) and 110 (type of scale). Character 26, coded as 1 (present) for *Sapperichthys*, is a highly homoplastic character with this state shared by several members of the three gonorynchiform families (i. e., Chanidae, Gonorynchidae, and Kneriidae). Character 110 [1] (modified ctenoid scale), presented by POYATO-ARIZA et al. (2010) as an autapomorphic character for the Gonorynchidae, in fact is only coded as present in *Notogoneus* and *Gonorynchus*. However, for *Sapperichthys* the state for this character is not clear, and for the other fossil gonorynchids included in the analyses, the state for this character is still unknown. The results obtained by POYATO-ARIZA et al. (2010) present character 123 (direct insertion of adductor mandibulae A2 far anteriorly on the anteromesial surface of the dentary); however, as expected, the state for this character is not codable in any of the fossils included in the analysis.

The results obtained with the DELTRAN optimization differ from those of POYATO-ARIZA et al. (2010) in the optimization of character 30 [1] (loose articulation between dentary and anguloarticular, with a posteriorly V-shaped dentary), and character 71 [0] (supraorbital bone present). Character 30 [1] (loose articulation between dentary and anguloarticular, with a posteriorly V-shaped dentary) is only exhibited by *Sapperichthys*, *Notogoneus*, and *Gonorynchus*, being reversed in the Middle Eastern gonorynchids which share state 0 (strong articulation between dentary and anguloarticular, dentary not V-shaped posteriorly) with the Chanidae and Kneriidae. Character 71 [1] (supraorbital absent) is only present in *Sapperichthys*, *Notogoneus*, *Gonorynchus*, and *Charitopsis*, with all of the other fossil and recent forms presenting state 0 (supraorbital bone present). On the other hand, the results of POYATO-ARIZA et al. (2010) present characters 44 [1] (mesethmoid extending anteriorly beyond the level of the anterior margin of the vomer), 110 [1] (modified ctenoid scale) (both states are not clear in *Sapperichthys*), and character 53 [1] (triangular opercle), which was used by the authors to diagnose the Gonorynchidae. However, *Sapperichthys chiapanensis* exhibits character 53 [0] (rounded opercle), thus differing from all other gonorynchids included in the analysis.

Our results recover the same phylogeny proposed by both GRANDE & GRANDE (2008b) and POYATO-ARIZA et al. (2010) for *Notogoneus*, *Gonorynchus* and the Middle Eastern gonorynchids; however, we suggest

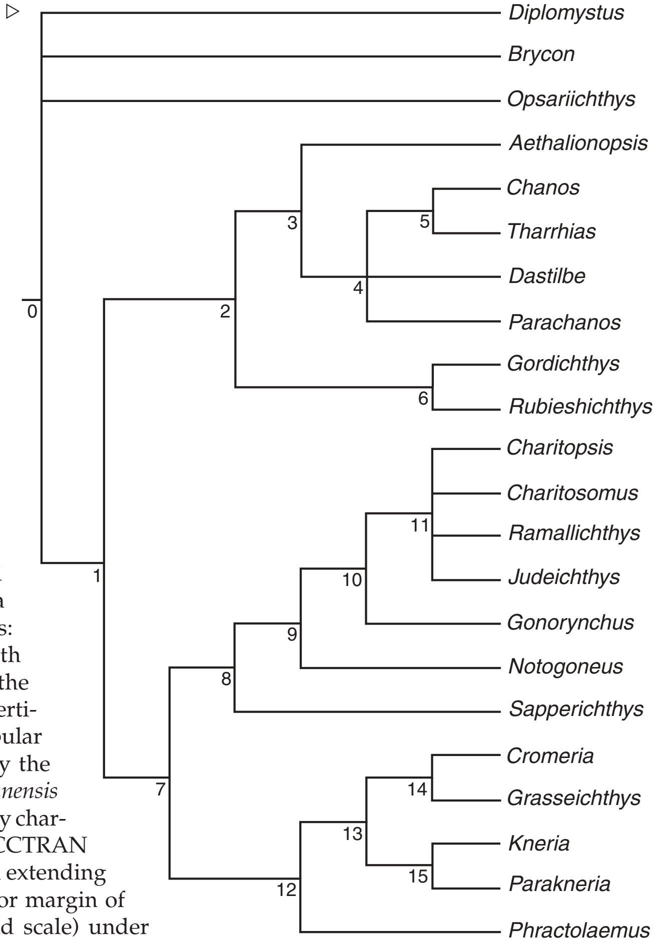

Fig. 7.
Strict consensus tree of the Gonorynchiformes with the inclusion of *Sapperichthys chiapanensis*, gen. et sp. nov. Nodes and node support: [A] indicates autapomorphy, [R] indicates reversion, and the number in brackets indicates character states other than 1. **Node 7**, Gonorynchoidei: 3 [2,A], 29, 32 [A], 41 [2,A], 45, 49 [A], 51 [A], 56 [A], 69 [A], 81, 88, 94, 99, 101, 127 [A]. With DELTRAN it also presents characters 6 and 68, and lacks characters 29, 45, and 99. **Node 8**, Gonorynchidae: 9 [A], 22 [A], 26, 30, 40 [A], 44, 71, 110 [A], 113 [A], and 128 [A]. With DELTRAN it also presents characters 29 and 45, and lacks characters 22, 26, 44, 110, 113, and 128. **Node 9**, Gonorynchidae, except for *Sapperichthys chiapanensis*, gen. et sp. nov.: 53 [A]. With DELTRAN it also presents characters 44 [R,1] and 110.

Sapperichthys chiapanensis as the most basal member of the Gonorynchidae, based on a unique combination of characters such as: expanded supraneurals, not in contact with each other, and loosely articulated with the neural arches; a rounded opercle; and a vertically oriented and triangular hyomandibular head. Additionally, the group formed by the Gonorynchidae minus *Sapperichthys chiapanensis* (Fig. 7, Node 9) is diagnosed exclusively by character 53 [1] (triangular opercle) under ACCTRAN and also by characters 44 [1] (mesethmoid extending anteriorly beyond the level of the anterior margin of the vomer) and 110 [1] (modified ctenoid scale) under DELTRAN optimization.

However it is crucial to note that the caudal endoskeleton is not preserved in the studied specimens of *Sapperichthys*. POYATO-ARIZA et al. (2010) stated that features of the caudal endoskeleton play an important role in assessments of relationships of the Gonorynchidae and, based on the reinterpretation of the caudal endoskeleton provided by GRANDE & GRANDE (2008a) for *Notogoneus osculus*, they proposed a new arrangement for the Gonorynchidae with *Notogoneus* as the most basal member of the Gonorynchidae, followed by *Gonorynchus* as the sister-taxon of the Middle Eastern gonorynchids. The distribution of the caudal characters was the same as that found by POYATO-ARIZA et al. (2010) for *Notogoneus*, *Gonorynchus*, and the other gonorynchids, and thus was mainly influenced by the reinterpretation of the caudal endoskeleton of *Notogoneus* presented by GRANDE & GRANDE (2008a).

Historical Biogeography

The temporal and spatial distribution of the Gonorynchidae is documented by fossil forms from Europe, Asia, Australia, and Africa, ranging from the Upper Cretaceous to the Eocene, and extant forms known from the Indian, Pacific, and Southeastern Atlantic Oceans (Fig. 8).

The Upper Cretaceous record of the Gonorynchidae comprises the Middle Eastern gonorynchids, which are represented by five marine fossil genera collected from the Congo, Germany, West Bank, and Lebanon. The Cretaceous gonorynchids include *Ramallichthys orientalis* GAYET, 1982, and *Judeichthys haasi* GAYET, 1985, described from marine sediments of Ramallah (West Bank), *Charitopsis spinosus* GAYET, 1993b, from Hakel (Lebanon), the genus *Charitosomus* VON DER MARCK, 1885, represented by the

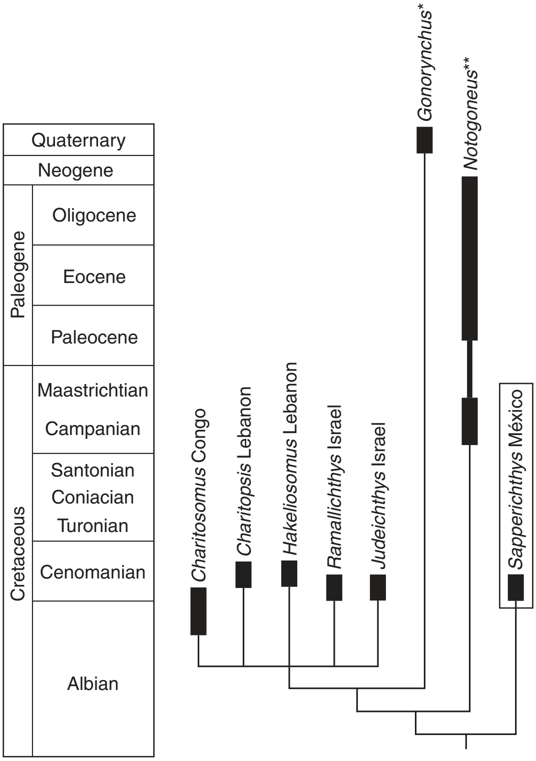

Fig. 8.
Area cladrogram and stratigraphic distribution of the Gonorynchidae based on Figure 7, with the inclusion of *Sapperichthys* gen. nov. * Indian, Pacific, and Southeastern Atlantic Oceans; ** Europe, North America, China, and Australia.

species *C. hermani* (TAVERNE, 1976), from the Albian–Cenomanian of Kipala (Congo), *C. lineolatus* (PICTET & HUMBERT, 1866), from Lebanon, *C. major* (WOODWARD, 1901), from the Santonian of Sahel Alma (Lebanon), and *C. formosus* VON DER MARCK, 1885, from the Campanian–Maastrichtian of Baumberg (Germany), along with the genus *Hakeliosomus* (GAYET, 1993a), described originally as *Charitosomus hakelensis* (DAVIS, 1887), from the Cenomanian of Hakel (Lebanon), and *Notogoneus montanensis* GRANDE & GRANDE, 1999, from the Campanian of Montana (USA).

In the Paleogene, the widespread genus *Notogoneus* includes the type-species, *Notogoneus osculus* COPE, 1885, described from the Eocene of the Green River Formation, Wyoming (USA); *Notogoneus gracilis* SYTCHEVSKAYA, 1986, from the upper Paleocene/lower Eocene of Boltyshka Basin (Ukraine); *Notogoneus squamosseus* (BLAINVILLE, 1818), from the lower Oligocene of France; *Notogoneus cuvieri* (AGASSIZ, 1843), from the upper Eocene of Montmarte (France); *Notogoneus janeti* PRIEM, 1908, from the upper Eocene/lower Oligocene from France northeast of Paris; *Notogoneus longiceps* (MEYER, 1848) from the lower Miocene of Germany; and *Notogoneus parvus* HILLS, 1934, from the lower Oligocene of Southern Queensland (Australia). Additionally, undescribed species were recorded by WILSON (1980), who recorded the presence of scales and skull bones he ascribed to the genus *Notogoneus* from the Paleocene of the Paskapoo Formation, Alberta (Canada) and by GRANDE (1999), who recorded the presence of another species of *Notogoneus* from the Paleocene/Eocene of the Shandong Province (China).

The extant record of the Gonorynchidae comprises only the genus *Gonorynchus* SCOPOLI, 1777, which is a deep-water taxon that inhabits marine environments in the Indian, Pacific, and southeastern Atlantic Oceans, and is composed by five species: *Gonorynchus gonorynchus* LINNAEUS, 1766; *G. abbreviatus* TEMMINK & SCHEGEL, 1846; *G. moseleyi* JORDAN & SNYDER 1923; G. *forsteri* OGILBY 1911; and *G. greyi* RICHARDSON, 1845.

Sapperichthys chiapanensis, gen. et sp. nov., from the Cenomanian of Mexico, is the oldest record of the Gonorynchidae in North America, and it reinforces the relationships among the Cenomanian marine faunas at the extreme limits of the Occidental Tethys Ocean near the Lower/Upper Cretaceous boundary (Fig. 9). Furthermore, the basal position of *Sapperichthys chiapanensis* within the family suggests that the history of the entire family Gonorynchidae could be initially related to the opening of the Caribbean/Mediterranean Tethys, in a dispersalist scenario marked by a two-way faunal exchange between the oriental and occidental Tethys, and the eastern Pacific at least since the Middle Jurassic as proposed by ABERHAN (2001), and the posterior establishment of the North Atlantic Ocean. The same pattern is found for certain ammonites (SMITH 1983), bivalves (ABERHAN 2001, HALLAM 1983), some marine ichthyosaurs, plesiosaurs, and crocodiles (GASPARINI & FERNANDEZ 2005, GASPARINI et al. 2006, GASPARINI et al. 2007), as well as for the Gonorynchiformes (AMARAL & BRITO 2012), therefore corroborating a Tethyan origin not only for the Gonorynchidae as proposed by JERZMAÑSKA (1977) and GAUDANT (1993), but for the Gonorynchiformes as a whole. Beginning in the Paleocene, we suggest that there was a range expansion of the genus *Notogoneus*, across Northern Europe, Northern North America, Asia, and Australia, followed by a second expansion represented by the modern range of the genus *Gonorynchus* throughout the Indian, Pacific, and southeastern Atlantic Oceans.

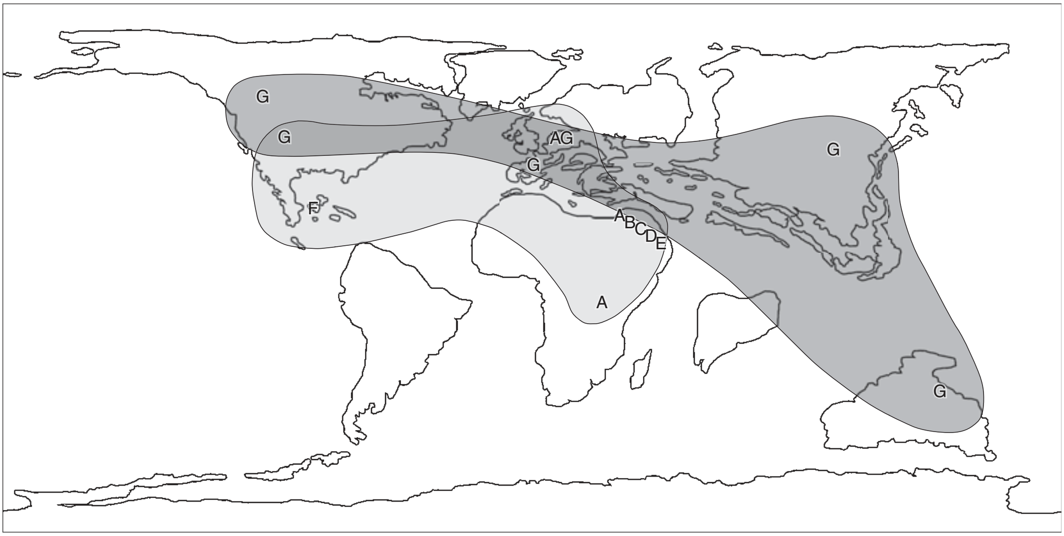

Fig. 9.
Cretaceous/Tertiary map and the distribution of fossil gonorynchids. The light gray area corresponds to the Late Cretaceous distribution of the genera: **A**, *Charitosomus*; **B**, *Charitopsis*; **C**, *Ramallichthys*; **D**, *Hakeliosomus*; **E**, *Judeichthys*; **F**, *Sapperichthys* gen. nov.; and **G**, *Notogoneus*. The dark gray area corresponds to the Paleocene-Eocene distribution of the genus **G**, *Notogoneus*.

Conclusions

Sapperichthys chiapanensis exhibits the following characters that support its inclusion within the Gonorynchiformes (sensu ROSEN & GREENWOOD 1970): the absence of orbitosphenoid and basisphenoid; the anterior neural arches expanded in the lateral plane, and the presence of three sets of intermuscular bones. Additionally, it exhibits the following characters that support its inclusion within the Gonorynchidae (sensu GRANDE & POYATO-ARIZA 1999): the elongate and narrow frontal except in the postorbital region, the presence of the endopterygoid and basibranchial toothplates filled with small conical teeth, and the typical morphology of the jaws.

Sapperichthys chiapanensis, gen. et sp. nov., is the most basal member of the Gonorynchidae, forming the sister-taxon of *Notogoneus* plus the group formed by *Gonorynchus* and the Middle Eastern gonorynchids, based on the characters such as: the presence of a rounded opercle with a spiny posterior border; a smooth subopercle; a vertically oriented and triangular hyomandibular head; a wide metapterygoid; a V-shaped dentary, loosely articulated with the anguloarticular; medially expanded supraneurals, not in contact with each other, and loosely articulated with the neural arches; about 40 vertebrae; and 11 dorsal fin rays.

Sapperichthys chiapanensis is the oldest record for the Gonorynchidae in North and Central America, reinforcing the relationships among the Cenomanian marine faunas between the extreme limits of the Tethys Ocean during the mid Cretaceous. These results corroborate a Tethyan origin for the family as proposed by JERZMAŃSKA (1977) and GAUDANT (1993), and for the Gonorynchiformes as a whole, since the historical biogeography of its sister-family Chanidae is also related with the evolution of the Tethys Ocean during the Pangea/Gondwana breakup.

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Appendix

This a list of characters modified from POYATO-ARIZA et al. (2010) exhibiting the character states for *Sapperichthys chiapanensis* gen. et sp. nov. in **bold**. For further discussion about the characters states, see that manuscript.

1. Orbitosphenoid: present [0]; **absent [1]**.
2. Basisphenoid: present [0]; **absent [1]**.
3. Pterosphenoids: well developed and articulating with each other [0]; slightly reduced, not articulating anteroventrally but approaching each other anterodorsally [1]; greatly reduced and broadly separated both anteroventrally and anterodorsally [2]. The character state is unknown in *Sapperichthys*.
4. Posterolateral expansion of exoccipitals: **absent [0]**; present [1].
5. Exoccipitals: posteriorly smooth with no projection above the basioccipital [0]; with a posterior concave-convex border, and a projection above the basioccipital [1]. The character state is unknown in *Sapperichthys*.
6. Cephalic ribs: absent [0]; present and all articulating with the exoccipitals [1]; present and articulating with both the exoccipitals and basioccipital [2]. The character state is unknown in *Sapperichthys*.
7. Brush-like cranial intermuscular bones: absent [0]; **present [1]**. POYATO-ARIZA et al. (2010) coded *Chanos* as lacking brush-like cranial intermuscular bones. Following ARRATIA & HUAQUIN (1995) and based on some specimens studied herein, we coded *Chanos* as having the state [1].
8. Nasal bone: small but flat [0]; just a tubular ossification around the canal [1]; absent as independent ossification [2]. The character state is unknown in *Sapperichthys*.
9. Frontals: wide through most of their length, narrowing anteriorly to form a triangular anterior border [0]; **elongate and narrow except in postorbital region [1]**; wide, anteriorly shortened, anterior border roughly straight [2]; roughly rectangular in outline, narrow throughout their length [3].
10. Interfrontal fontanelle: **absent [0]**; present [1].
11. Frontal bones: **paired in adult [0]**; co-ossified, with no median suture [1].
12. Foramen for olfactory nerve in frontal bones: **absent [0]**; present [1].
13. Relative position of the parietals: medioparietal (in full contact with each other along their midline) [0]; mesoparietal [1]; lateroparietal (completely separated from each other by the supraoccipital) [2]. Following ARRATIA (pers. obser.), and the description for the Kneriidae provided by POYATO-ARIZA et al. (2010), the character was re-coded as non-applicable (–) for *Kneria* and *Parakneria*. The character state is unknown in *Sapperichthys*.
14. Parietal portion of the supraorbital canal: absent [0]; present [1]. ARRATIA & BAGARINAO (2010) observed that the parietal branch of the supraorbital canal pierces the parietal in *Chanos*, therefore, following these authors we re-coded it to state [1]. The character state is unknown in *Sapperichthys*.
15. Parietals: large [0]; **reduced but flat and blade-like in shape [1]**; reduced to canal-bearing bones [2]; absent as independent ossifications [3].
16. Supraoccipital crest: **small, short in lateral view [0]**; long and enlarged, projected above occipital region and first vertebrae, forming a vertical, posteriorly deeply pectinated blade [1].
17. Foramen magnum: dorsally bounded by exoccipitals [0]; enlarged and dorsally bounded by supraoccipital [1]. The character state is unknown in *Sapperichthys*.
18. Mesethmoid: **wide and short [0]**; long and slender, with anterior elongate lateral extensions [1]; large, with broad posterolateral wing-like expansions [2]; elongate and thin [3]. DAVIS et al. (this volume, page 330) observed variation in mesethmoid morphology of *Kneria* and *Parakneria* considering the character in need of further investigation. We decided to delete it from our analysis due to the subjectivity of the state descriptions.
19. Wings (extensions) on lateral ethmoids: **absent [0]**; present [1].
20. Teeth in premaxilla, maxilla, and dentary: present [0]; **absent [1]**.
21. Premaxilla: **consisting of one solid portion [0]**; premaxilla consisting of two distinct portions, with a shorter, non-osseous element lying ventral to a much longer osseous portion, which in turn articulates with the maxilla [1].
22. Premaxillary "gingival-teeth": absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
23. Premaxilla: small, flat, and roughly triangular [0]; large, very broad, concave-convex, with long oral process [1]; narrow and elongated, its length more than one half of the length of the maxilla [2]. The character state is unknown in *Sapperichthys*.
24. Premaxillary ascending process: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
25. Dorsal and ventral borders of the maxillary articular process: straight or slightly curved [0]; very curved, almost describing an angle [1]. The character state is unknown in *Sapperichthys*.
26. Maxilary process for articulation with autopalatine: absent [0]; **present [1]**.
27. Posterior region of the maxilla: **slightly and progressively expanded to form a thin blade, with roughly straight posterior border [0]**; very enlarged, swollen to a bulbous outline, with curved posterior border [1].

28. Supramaxilla(e): present [0]; **absent [1]**.
29. Notch between the dentary and the angulo-articular bones: absent [0]; **present [1]**.
30. Articulation between dentary and angulo-articular: strong, dentary not V-shaped posteriorly [0]; **loose, with a posteriorly V-shaped dentary [1]**.
31. Notch in the anterodorsal border of the dentary: **absent [0]**; present [1].
32. Mandibular sensory canal: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
33. Inferior and superior enlarged retroarticular processes of mandible: **both absent [0]**; inferior retroarticular process present, superior retroarticular process absent [1]; both inferior and superior retroarticular processes present [2].
34. Quadrate with: **posterior margin smooth [0]**; elongated forked posterior process [1].
35. Quadrate mandibular articulation: **below or posterior to orbit, no elongation or displacement of quadrate [0]**; anterior to orbit, quadrate displaced but not elongated [1]; anterior to orbit, with elongation of the body of quadrate instead of displacement [2].
36. Symplectic: **elongated in shape but relatively short [0]**; very long, about twice the length of the ingroup [1]; absent as an independent ossification [2].
37. Symplectic and quadrate: **articulating directly with each other [0]**; separated trough cartilage [1]; no contact due to the absence of symplectic [2].
38. Metapterygoid: **large, broad, and in contact with quadrate and symplectic through cartilage [0]**; reduced to a thin rod [1].
39. Dermopalatine: present [0]; **absent [1]**.
40. A patch of about 20 conical teeth on endopterygoids and basibranchial 2: absent [0]; **present [1]**.
41. Ectopterygoids: well developed, ectopterygoid overlapping with the ventral surface of the autopalatine by at least 50 % [0]; well developed, with three branches in lateral view, reduced but direct contact with autopalatine [1]; **reduced, articulating with the ventral surface of the autopalatine by at most 10 % through cartilage, resulting in a loosely articulated suspensorium [2]**; absent as distinct ossifications [3].
42. Teeth on vomer and parasphenoid: **absent [0]**; present [1].
43. Anterior portion of vomer: **horizontal [0]**; anteroventrally inclined nearly vertical [1]; dorsally curved [2].
44. Spatial relationship between vomer and mesethmoid anteriorly: vomer and mesethmoid ending at about the same anterior level [0]; mesethmoid extending anteriorly beyond the level of anterior margin of vomer [1]; vomer extending anteriorly beyond the level of anterior margin of mesethmoid [2]. The character state is unknown in *Sapperichthys*.
45. Articular head of hyomandibular bone: double, with both articular surfaces placed on the dorsal border of the main body of the bone [0]; **double, with the anterior articular surface forming a separate head from the posterior articular surface [1]**.
46. Metapterygoid process of hyomandibular bone: **absent [0]**; present anterior [1]; present, ventral [2].
47. Ossified interhyal: present [0]; absent as an independent ossification [1]. Following DAVIS et al. (this volume, page 330) for *Kneria* and *Parakneria*, and based on observed specimens of *Chanos*, the interhyal is regarded herein as absent in all three genera. The charater was re-coded to state [1] in all three genera. The character state is unknown in *Sapperichthys*.
48. Teeth on fifth ceratobranchial: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
49. First basibranchial in adult specimens: ossified [0]; unossified [1]. The character state is unknown in *Sapperichthys*.
50. Fifth basibranchial in adult specimens: cartilaginous [0]; ossified [1]. The character state is unknown in *Sapperichthys*.
51. First pharyngobranchial in adult specimens: ossified [0]; unossified [1]. The character state is unknown in *Sapperichthys*.
52. Size of opercular bone: **normal, about one quarter the head length [0]**; expanded, at least one third of the head length [1].
53. Shape of opercular bone in lateral view: **rounded/oval [0]**; triangular [1]; squarish or square [2]. We added character state [2] for the square-shaped opercular bone as reported by DAVIS et al. (this volume, page 330), for *Parakneria*, and re-coded *Kneria* as polymorphic with the states [0] and [2].
54. Opercular spines: absent [0]; **present [1]**.
55. Opercular apparatus on external surface of operculum: **absent [0]**; present [1].
56. Opercular borders: free from side of head [0]; partly or almost completely connected to side of the head with skin [1]. The character state is unknown in *Sapperichthys*.
57. Angle formed by preopercular limbs: **obtuse [0]**; approximately straight [1]; acute [2].
58. Posterodorsal limb of preopercular bone: **well developed [0]**; reduced, correlated with expansion of anteroventral limb that meets its fellow along the ventral midline [1].

59. Ridge on anteroventral limb of preopercular bone: **absent [0]**; present [1].
60. Preopercular expansion: absent, preopercular not enlarged [0]; present, restricted to the posteroventral corner [1]; present in posteroventral corner and part of the posterodorsal limb [2]; present in anteroventral limb only [3].
61. Suprapreopercular bone: **absent [0]**; present as a relatively large, flat bone [1]; present as tubular ossification(s) [2].
62. Spine on posterior border of subopercular bone: **absent [0]**; present [1].
63. Major axis of subopercular bone in lateral view: **inclined [0]**; subhorizontal [1]; subvertical [2].
64. Subopercular clefts: **absent [0]**; present [1].
65. Interopercular bone: **relatively broad and positioned medioventral to preopercular bone [0]**; reduced to a long thin spine and positioned mediodorsal to preopercular bone [1]; reduced to a long thin spine and positioned lateroventral to preopercular bone [2].
66. Spine on posterior border of interopercular bone: **absent [0]**; present [1].
67. Posterodorsal ascending process of interopercular bone: **absent [0]**; present [1].
68. Number of infraorbitals: five or more [0]; four [1]; three or fewer [2]. The character state is unknown in *Sapperichthys*.
69. Infraorbital bones not including lacrimal: well developed [0]; **reduced to small, tubular ossifications [1]**; hypertrophied [2].
70. Lacrimal: flat and comparable in lenght to subsequent infraorbitals [0]; tube-like and extremely long, without keel [1]; flat, long and large, with keel near lower edge [2]; long and large, with spines and crests [3]. The character state is unknown in *Sapperichthys*.
71. Supraorbital: present [0]; **absent [1]**.
72. Two anteriormost vertebrae: as long as posterior ones [0]; shorther than posterior ones [1]. The character state is unknown in *Sapperichthys*.
73. Second abdominal centrum: as long as first [0]; shorther than first [1]. GRANDE & ARRATIA (2010) observed the variability of this character in the Kneriidae presumably associated with sexual dimorphism. Therefore we consider this character in need of further investigation and we prefer to delete it from our analysis. The character state is unknown in *Sapperichthys*.
74. Autogenous neural arch anterior to arch of first vertebra: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
75. Neural arch of first vertebra and exoccipitals: separate [0]; **in contact [1]**.
76. Neural arch of first vertebra and supraoccipital: separated [0]; in contact [1]. The character state is unknown in *Sapperichthys*.
77. Spine on the neural arch of first vertebra: present, well developed [0]; present but reduced [1]; absent [2]. The character state is unknown in *Sapperichthys*.
78. Anterior neural arches: **no contact with adjoining arches [0]**; abutting adjoining arches medially, without overlap [1]; overlapping contact with adjoining arches medially [2].
79. Unmodified neural arches anterior to dorsal fin in adults: **fused to centra [0]**; autogenous, at least laterally [1].
80. Neural arches of vertebrae posterior to the dorsal fin in adults: **fused to centrum [0]**; autogenous, at least laterally [1].
81. First two anterior parapophyses: autogenous [0]; fused to centra [1]. The character state is unknown in *Sapperichthys*.
82. Rib on third vertebral centrum: similar to posterior ones [0]; **widened and shortened [1]**; modified into Weberian apparatus [2].
83. Paired intermuscular bones consisting of three series: epipleurals, epicentrals, and epineurals: absent [0]; **present [1]**.
84. Anterior (first six) epicentral bones: **unmodified, no differences in size from others [0]**; highly modified, much larger than posterior ones [1]; epicentrals in anterior vertebrae absent [2].
85. Size an arrangement of anterior supraneurals (whatever the number present): **large, separate from each other if more than one supraneural present [0]**; larger, in contact with neighbors if more than one supraneural present [1]; supraneurals greatly reduced in size [2].
86. Posterior process on the posterior border of first supraneural: **absent [0]**; present [1].
87. Number of supraneurals: **several supraneurals in long series [0]**; two or fewer supraneurals [1].
88. Postcleithra: present [0]; **absent [1]**.
89. Lateral line and supracleithrum: supracleithrum pierced through dorsal region [0]; supracleithrum pierced all through its length [1]; lateral line does not pierce supracleithrum. We re-coded both *Kneria* and *Parakneria* (state [2]) following DAVIS et al. (this volume, page 330), who observed that the lateral line does not pierce the supracleithrum in both genera. The character state is unknown in *Sapperichthys*.

90. Fleshy lobe of paired fins: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
91. Caudal fin morphology: elongated, posteriorly forked [0]; higher than long, slightly incurved posteriorly [1]; crescent-shaped [2]. The character state is unknown in *Sapperichthys*.
92. Fringing fulcra in dorsal lobe of caudal fin: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
93. Caudal scute: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
94. Ural centra, preural centrum 1, and uroneural 1: autogenous [0]; fused [1]; fused except for ural centrum 2, which is autogenous [2]. The character state is unknown in *Sapperichthys*.
95. Neural arch and spine of preural centrum 1: both well developed, spine about half as long as preceding ones [0]; arch complete and closed, spine rudimentary [1]; arch open, no spine [2]. DAVIS et al. (this volume, page 331) observed variation of the character in *Parakneria*. Therefore, and following those authors, we re-coded it as polymorphic exhibiting both states [1] and [2]. *Chanos* was re-coded as presenting state [1] based on observed specimens. The character state is unknown in *Sapperichthys*.
96. Uroneurals: arranged in a linear series [0]; arranged in a double series [1]. The character state is unknown in *Sapperichthys*.
97. Number of uroneurals: three [0]; two or one [1]; none [2]. This character was deleted from our analysis due to the fact that there are no gonorynchiform which lacks uroneurals. The character state is unknown in *Sapperichthys*.
98. Anterior extent of first uroneural: to anterior end of first preural [0]; to anterior end of second preural [1]; to anterior end of third preural [2]; uroneural fused to caudal fin complex [3]. The character state is unknown in *Sapperichthys*.
99. Uroneural two and second ural centrum: in contact [0]; separated [1]; uroneural two absent [2]. The character state is unknown in *Sapperichthys*.
100. Parhypural and preural centrum 1: independent in adults [0]; fused only in large adults [1]; fused since early ontogenetic stages [2]. The character state is unknown in *Sapperichthys*.
101. Reduction in the number of hypurals: six [0]; fewer than six [1]. The character state is unknown in *Sapperichthys*.
102. Hypurals 1 and 2: independent [0]; partly fused to each other [1]; totally fused to each other [2]. The character state is unknown in *Sapperichthys*.
103. Hypural 1 and terminal centrum: articulating [0]; separated by a hiatus [1]; fused [2]. The character state is unknown in *Sapperichthys*.
104. Hypural 2 and terminal centrum: fused [0]; articulating [1]. The character state is unknown in *Sapperichthys*.
105. Hypural 5: of comparable size to preceding ones [0]; considerably larger [1]. The character state is unknown in *Sapperichthys*.
106. Hypural 5 (plus 6 if present) and second ural centrum (of diural terminology): separate [0]; articulating [1]. Among the studied taxa, the apomorphic state is only found in *Rubiesichthys*. Regarding these problems we consider this character in need of further investigation and we decided to delete it from our analysis. The character state is unknown in *Sapperichthys*.
107. Haemal arch and preural centrum 2: fused [0]; independent [1]. The character state is unknown in *Sapperichthys*.
108. Posterolateral process of caudal endoskeleton: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
109. Scales on body: **present [0]**; absent [1].
110. Type of scales: cycloid [0]; modified ctenoid [1]. The character state is unknown in *Sapperichthys*.
111. Lateral line: not extending to posterior margin of hypurals [0]; extending to posterior margin of hypurals [1]. The character state is unknown in *Sapperichthys*.
112. Intermandibularis: mainly attaching on the dentary [0]; exclusively attaching to angulo-articular [1]. The character state is unknown in *Sapperichthys*.
113. Protractor hyoidei: not inserting on coronoid process [0]; inserting on coronoid process [1]. The character state is unknown in *Sapperichthys*.
114. Hyohyoideus inferioris of both sides: mostly overlapping each other [0]; mostly mixing mesially with each other [1]. The character state is unknown in *Sapperichthys*.
115. Hyohyoideus abductor: not attaching on pectoral girdle [0]; with significant part of its fibers attaching on pectoral girdle [1]. The character state is unknown in *Sapperichthys*.
116. Adductor profundus: not subdivided into different sections [0]; subdivided into different sections [1]. The character state is unknown in *Sapperichthys*.
117. Attachment of adductor profundus: on first pectoral ray only [0]; on first and second pectoral rays [1]. The character state is unknown in *Sapperichthys*.

118. Most lateral bundles of adductor mandibulae: inserting on mandible and/or primordial ligament [0]; attaching also, or even exclusively, on other bones such as the maxilla and the premaxilla [1]. The character state is unknown in *Sapperichthys*.
119. Position of adductor mandibulae A1-OST: mostly horizontal [0]; with a peculiar anterior portion almost perpendicular to its posterior portion [1]. The character state is unknown in *Sapperichthys*.
120. Section A2 of adductor mandibulae: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
121. Several small tendons branching off from adductor mandibulae A2: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
122. Peculiar adductor mandibulae A1-OST-M: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
123. Direct insertion of adductor mandibulae A2 far anteriorly on anteromesial surface of dentary: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
124. Dilatator operculi: mainly mesial and/or dorsal to adductor mandibulae A2[0]; markedly lateral to A2[1]. The character state is unknown in *Sapperichthys*.
125. Peculiar tendon of adductor mandibulae A2 running perpendicular to main body of this section and connecting it to anteroventral surface of quadrate: absent [0]; present [1]. The character state is unknown in *Sapperichthys*.
126. Distinct section A3 of adductor mandibulae Aω: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
127. Adductor mandibulae Aω: present [0]; absent [1]. The character state is unknown in *Sapperichthys*.
128. Adductor arcus palatini: not inserting on preopercle [0]; inserting also on preopercle [1]. The character state is unknown in *Sapperichthys*.
129. Levator arcus palatini: not divided [0]; divided into two well-differentiated bundles [1]. The character state is unknown in *Sapperichthys*.
130. Origin of dilatator operculi: on ventrolateral surface of neurocranium [0]; on dorsal margin of cranial roof [1]. The character state is unknown in *Sapperichthys*.

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