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The Late Cretaceous chimaeroid fish, *Ischyodus bifurcatus* Case (Chondrichthyes: Holocephali), from California, USA, and its paleobiogeographical significance

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Abstract. A nearly complete right mandibular tooth plate of *Ischyodus bifurcatus* Case (Holocephali: Chimaeroidei) is reported from the Point Loma Formation (upper Campanian) of the Upper Cretaceous Rosario Group in southern California, USA. The individual is estimated to have measured nearly 1 m in total body length. Remains of *I. bifurcatus* have been reported from marine rocks deposited in epicontinental seas and continental shelf paleoenvironments of temperate latitudes in the Northern Hemisphere. Previous records of the species consist of specimens from Santonian to Maastrichtian strata of the US (Delaware, New Jersey, North Carolina, Georgia, Alabama, Arkansas, Montana, and Wyoming), Sweden, and European Russia. The tooth plate described herein is the first verifiable record of *I. bifurcatus* from California, and, more significantly, represents the only known definite Mesozoic record of *Ischyodus* from the entire North Pacific region.

Key words: chimaeroid fish, *Ischyodus*, Late Cretaceous, North Pacific, tooth plate

Introduction

Chimaeriformes (so-called 'ratfishes' or 'ghostsharks') includes holocephalian cartilaginous fishes with a durophagous lifestyle (Stahl, 1999). Extant taxa in this order are represented by three families, six genera, and approximately 50 species (Didier *et al.*, 2012; Weigmann, 2016), including forms that inhabit both deep water (Rhinochimaeridae and Chimaeridae) and nearshore marine environments (Callorhinchidae). In the fossil record, principal anatomical elements used for chimaeroid taxonomy and phylogenetic research are tooth plates, which occur as two pairs in the upper jaw (vomerine and palatine tooth plates) and one pair in the lower jaw (mandibular tooth plates). The oldest chimaeroid fossils occur in upper Triassic strata (Stahl, 1999). The clade reached its maximum diversity in the mid-Cretaceous (Newton, 1878; Popov and Machalski, 2014). The most common chimaeroid genus in the Cretaceous, as well as in the entire Mesozoic, is *Ischyodus* Egerton, 1843, a taxon ranging from the mid-Jurassic to Miocene and consisting of 39 nominal species (Stahl, 1999; Hoganson and Erickson, 2005). Although exceptionally rare in the fossil record, complete and nearly complete skeletons of *Ischyodus* (e.g. Stahl, 1999, fig. 136A, B) show that the extinct genus included relatively large forms (at least 40–150 cm in estimated total body length) and was morphologically similar to the extant genus *Callorhinchus* or 'elephantfish' (Popov *et al.*, 2013).

The Late Cretaceous record of *Ischyodus* consists of eight nominal species (Stahl, 1999; Hoganson and Erickson, 2005). Some species of *Ischyodus* possess a bifurcated median tritor on their mandibular tooth plates, like *I. bifurcatus* Case, 1978, from the Santonian to Maastrichtian, and *I. rayhaasi* Hoganson and Erickson, 2005, and *I. yanshini* Averianov, 1991, from the Campanian to Maastrichtian (see Appendix 1). The species with a bifurcated median tritor constitute a Late Cretaceous '*bifurcatus*-group' that is distinct from a group of *Ischyodus* with a simple non-forked mandibular median tritor, such as *I. lonzeensis*, *I. gubkini*, and *I. thurmanni* from the Late Cretaceous, as well as *I. dolloi* from the Paleocene.

Ischyodus latus, *Ischyodus* sp., and *I.* aff. *bifurcatus* from the Albian to Cenomanian described by Newton (1878), Nessov (1997), and Popov and Machalski (2014), respectively, exhibit a prominent crushing dentition and even stronger 'bifurcation' on their mandibular median tritor than that of the '*bifurcatus*-group.' However, the taxonomic status of these three species awaits reexamination (Popov and Machalski, 2014).

Herein, we report the first verified occurrence of *Ischyodus bifurcatus* from the Campanian of southern California, USA (Figure 1A). The specimen is a tooth plate housed at the San Diego Natural History Museum (SDNHM) and is catalogued as SDNHM 25417. This specimen is noteworthy because it represents the first record of *I. bifurcatus* from western North America as well as the first and only known definite Mesozoic record of *Ischyodus* from the entire North Pacific region.

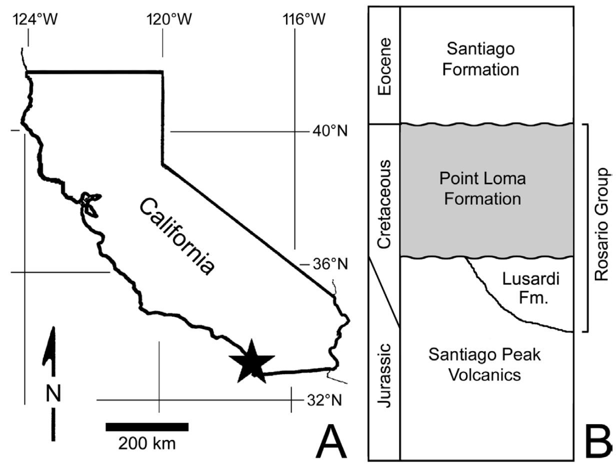

Figure 1. Geographic location and stratigraphic position of chimaeroid tooth plate described in the present study. **A,** map of California, USA, showing fossil chimaeroid locality (star symbol); **B,** simplified stratigraphic column of San Diego area (southern California) showing formations of Upper Cretaceous Rosario Group (Point Loma Formation where fossil chimaeroid was collected highlighted in gray), that overlies metavolcanic Upper Jurassic–Lower Cretaceous Santiago Peak Volcanics, and that unconformably underlies estuarine strata of middle–upper Eocene Santiago Formation.

Geological setting and associated fossils

The chimaeroid tooth plate, SDNHM 25417, was collected from a blue-gray, massive, sandy marine mudstone stratum in the lower part of the Point Loma Formation exposed in Carlsbad, San Diego County (Figure 1B). At Carlsbad, the Point Loma Formation consists of a relatively thin (~23 m) sequence of thickly to thinly bedded, massive to locally flaggy mudstones and siltstones with occasional interbeds and lenses of fine- to medium-grained, locally cemented sandstone (Sliter, 1968). Generally, the Point Loma Formation in the Carlsbad area unconformably overlies Upper Cretaceous fanglomerates of the Lusardi Formation. However, the formation locally rests nonconformably on Upper Jurassic to Lower Cretaceous metavolcanic rocks of the Santiago Peak Volcanics (Coombs and Deméré, 1996). A high-relief unconformity separates the Point Loma Formation from overlying estuarine strata of the middle to upper Eocene Santiago Formation. Bukry (1994) described nannofossil floras from the Carlsbad section of the Point Loma Formation and reported that the section contains the Zone CC21 to CC22 boundary within the late Campanian (~75 Ma). Sliter (1968) described planktonic and benthonic foraminifers from the Carlsbad Cretaceous section and assigned them to the *Globotruncana rosetta* Zone, also of late Campanian age. Sliter (1968) also suggested that deposition of the Carlsbad strata occurred on the continental shelf.

Widely dispersed and well preserved fossils of marine invertebrates occur in the Carlsbad section of the Point Loma Formation, including remains of crustaceans (*Icriocarcinus xestos*), echinoids, cephalopods (*Anapachydiscus peninsularis*, *Pachydiscus catarinae*, *Anglonautilus catarinae*, and *Baculites* sp.), gastropods (*Anchura gibbera* and *Bernaya* sp.), and bivalves (*Indogrammatodon* sp., *Pinna* sp., *Spondylus rugosus*, and *Crassatella* sp.) (Bishop, 1988; Loch, 1989; Groves, 1990; Squires and Saul, 2001). Vertebrate fossils from the Carlsbad section consist of teeth, otoliths, and axial skeletal elements of actinopterygians, a peripheral plate of a chelonian (SDNHM 31366), and skeletal remains of ornithischian dinosaurs, including an ankylosaurid ankylosaur *Aletopelta coombsi* (Coombs and Deméré, 1996; Ford and Kirkland, 2001) and unidentified hadrosaurs (Hilton, 2003).

Systematic paleontology

Besides SDNHM, specimens in the following two institutions are referred to in this paper: the Regional Museum of Physical Geography, Saratov State University (SSU), Russia, and the University of Montpellier (UM), France. Descriptive terms and measurements of chimaeroid tooth plates used in this study (Figure 2) follow Popov (1999, 2003), Popov and Efimov (2012), and Popov and Machalski (2014) by building on the schemes presented by Newton (1878), Ørvig (1985), Patterson (1992), and Stahl (1999). Higher-level taxonomy (superfamily and above) follows Nelson *et al.* (2012). The family 'Edaphodontidae' Owen, 1846, is here considered to represent a collective taxonomic unit in need of revision (see Popov and Beznosov, 2006; Popov and Machalski, 2014). Its composition and relationships with other chimaeroid

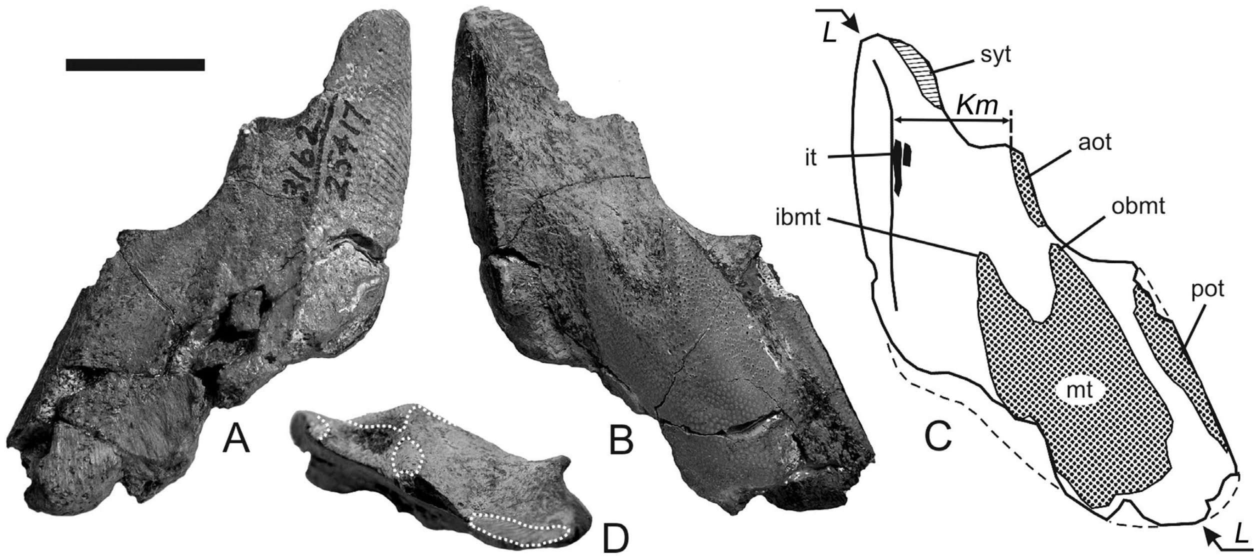

Figure 2. Right mandibular tooth plate of *Ischyodus bifurcatus* (SDNHM 25417) from upper Campanian of southern California, USA. **A,** basal view; **B,** occlusal view; **C,** line drawing interpretation of tooth plate in occlusal view (cf. Figure 2B) with identified tritors and type of pleromin fill (dashed lines = restored parts); **D,** mesial (symphysial) view. Anatomical abbreviations: aot, anterior outer tritor; ibmt, inner branch of median tritor; it, inner tritor(s); mt, median tritor; obmt, outer branch of median tritor; pot, posterior outer tritor; st, symphysial tritor. Measurement abbreviations: *L*, maximum mesio-distal length of tooth plate; *Km*, distance between symphysial margin and anterior outer tritor ('reference width' of Popov and Machalski, 2014). Symbols for tritor infilling: dotted or solid black, vascular pleromin; horizontal parallel lines, laminated pleromin. Scale bar = 1 cm.

families require phylogenetic analysis, which is beyond the scope of the present study.

Class Chondrichthyes Huxley, 1880
Subclass Holocephali Bonaparte, 1832
Superorder Holocephalimorpha Nelson, 2006
Order Chimaeriformes Obruchev, 1953
Suborder Chimaeroidei Patterson, 1965
Superfamily Callorhinchoidea Garman, 1901
Family 'Edaphodontidae' Owen, 1846
Genus ***Ischyodus*** Egerton, 1843

Type species.—*Chimaera townsendi* Buckland, 1835; Upper Jurassic (Tithonian), southern England.

Ischyodus bifurcatus Case, 1978

Figure 2

Ischyodus brevirostris Egerton. Davis, 1890, p. 414, pl. XLII, figs. 12, 13, 15 (*non* fig. 14 = *Amylodon* sp.).
Edaphodon sp. Case, 1967, p. 8, fig. 33.
Ischyodus bifurcatus Case, 1978, p. 21, pl. 1, figs. 1–4; Case, 1979, p. 226, pl. 2, figs. 1–3; Case and Schwimmer, 1992, p. 347, fig. 2; Popov and Ivanov, 1996, p. 56, fig. 2; Stahl, 1999, p. 132; Panteleyev *et al.*, 2004, p. 117; Averianov and Popov, 2014, p. 327; Cicimurri and Ebersole, 2014, p. 10, fig. 8A–D, *non* fig. 9A–C (*Edaphodon* sp.); Cicimurri and Ebersole, 2015, p. 21, fig. 11(4); Zverkov *et al.*, 2017, p. 2.
Ischyodus cf. bifurcatus Case. Robb, 1989, p. 81, fig. 13A, B, ?C; Averianov and Popov, 1995, p. 661; Nessov and Averianov, 1996, p. 16.
Ischyodus bifurcatus? Case. Nessov and Averianov, 1996, p. 16.
Ischyodus sp. Yarkov, 2001, p. 57.

Material.—SDNHM 25417, a nearly complete right mandibular tooth plate, collected in February 1984 by R. A. Cerutti.

Locality.—SDNHM Locality 3162B: Carlsbad, San Diego County, California. The locality was discovered during the development of the Carlsbad Research Center in a trench now covered by Faraday Avenue.

Stratigraphic horizon.—A mudstone stratum in the lower part of the Point Loma Formation (additional stratigraphic data are on file at SDNHM). Bukry (1994) assigned this stratigraphic section to coccolith zones CC21 and CC22, late Campanian.

Description.—SDNHM 25417 measures 47 mm in maximum mesiodistal length ('*L*' in Figure 2C) and 11 mm between the symphysial margin and anterior outer tritor ('*Km*' in Figure 2C; = 'reference width' of Popov and Machalski, 2014). The specimen is a medium-sized, moderately robust but flat mandibular plate with a moderately developed mandibular beak. The distribution of tritors on the occlusal side is typical of *Ischyodus*, comprising the (1) symphysial tritor, (2) anterior outer tritor, (3) posterior outer tritor, (4) median tritor, and (5) double inner tritors. The symphysial tritor is narrow and low in cross section, and primarily consists of laminated pleromin, but is laterally flanked by vascular pleromin (up to one-fourth of the tritor width). The pleromin body of the symphysial tritor is visible in basal view due to taphonomic abrasion in which traces of descending lamina are missing because of the abraded state (Figure 2A). All the remaining non-symphysial tritors show infilling of vascular (tubular) pleromin. The anterior and posterior outer tritors are mesiodistally elongated, with the posterior tritor being slightly wider and situated distally compared to the anterior tritor. The three labially positioned tritors (i.e., symphysial, anterior outer, and posterior outer tritors) protrude along the labial margin, defining two prominent concavities along the plate margin. The large, centrally placed median tritor is 'compound' in cross section (*sensu* Popov and Machalski, 2014) and is bifurcated anteriorly to form equal-sized, moderately developed, well separated inner and outer branches. The inner branch is well separated from the nearly straight symphysial margin of the tooth plate and is located slightly distally with respect to the anterior tip of the outer branch. The two inner tritors are small and parallel one another along the symphysial margin of the plate, and their vascular pleromin is compact without visible tubes. The inner tritor is positioned at the same level as the mesial extremity of the anterior outer tritor located laterally.

Taxonomic remarks.—SDNHM 25417 has a relatively large median tritor that constitutes a major crushing component of the mandibular plate. The position of the median tritor with respect to other tritors and the anterior bifurcation of the median tritor are consistent with those of the holotype of *Ischyodus bifurcatus* (UM 334) described by Case (1978). Previous studies have suggested that the median tritor of *I. bifurcatus* represents fusion of the medial and 'internal posterior' (= posterior inner) tritors (e.g. Case, 1978, 1979; Case and Schwimmer, 1992; Stahl, 1999). However, some Jurassic and mid-Cretaceous species of *Ischyodus* show varying degrees of development of the inner branch of the median tritor (e.g. Popov and Machalski, 2014, fig. 4C) in which 'bifurcation' without any tritor fusion (seen in *I. thurmanni*) is interpreted to be the plesiomorphic condition. Because of the wide morphological variation of the median tritor, with more or less prominent bifurcation in multiple Jurassic and Cretaceous species of *Ischyodus* (e.g. *Ischyodus egertoni*, *I. emarginatus*, and *I. latus*: Popov and Machalski, 2014), bifurcation could have evolved independently in multiple Mesozoic clades of *Ischyodus* besides the species categorized into the '*bifurcatus*-group' (see Introduction and Discussion herein).

The holotype of *Ischyodus bifurcatus* from the early or middle Maastrichtian has an additional small median tritor in the distal part of the plate between the median and posterior outer tritors (Case, 1978, pl. 1, fig. a), although this character is not specifically described in Case's (1978) original species diagnosis. Russian specimens (SSU collection: EVP, personal observation) also show variation in the total number of additional small median tritors (up to 5), although additional tritors appear to be more common in specimens from younger (e.g. Maastrichtian: typically 1 to 5 additional median tritors) deposits than older (e.g. Campanian: typically 0 to 3 additional median tritors) deposits. SDNHM 25417 from the Campanian lacks such additional median tritors, which is consistent with the temporal trend noted above.

Davis (1890) described and figured several tooth plates of *Ischyodus bifurcatus* from the Campanian of Sweden under the name *I. brevirostris* Newton (Agassiz, 1843). These specimens show clear bifurcation of the mandibular median tritor (Davis, 1890, pl. XLII, figs. 12, 13, 15) and do not differ significantly from tooth plates commonly referred to *I. bifurcatus* including SDNHM 25417. All the Swedish specimens illustrated by Davis (1890), except an incomplete vomerine plate (Davis, 1890, pl. XLII, fig. 14), are identified here as *I. bifurcatus*. The vomerine plate is similar to previously undescribed vomerine specimens (SSU 154/628) of a rhinochimaerid, *Amylodon karamysh* Averianov and Popov, 1995, from the Campanian of the Saratov region of Russia, and we therefore assign the Swedish vomerine plate to *Amylodon* sp.

Discussion

The holotype of *Ischyodus bifurcatus* is a large mandibular plate (L = 82 mm, Km = 17 mm), that is nearly twice the size of SDNHM 25417 (L= 47 mm, Km = 11 mm). Isolated mandibular plates (n = 40+) of this species from the Campanian Rybushka Formation in the Saratov and Volgograd regions of Russia, also show a considerably wide size range (e.g. L = *ca.* 36 to *ca.* 75 mm, Km = 6 to 25 mm; see Figure 2C), although their tritor pattern is relatively consistent (SSU collection: EVP, personal observation). Examination of two illustrated nearly complete skeletons of *Ischyodus* (*I. quenstedti* and *I. avitus*) by Stahl (1999, fig. 136A, B) reveals that the ratio between the L value and total body length (TL, that includes the elongate rostrum and tail) is 1:21. Whether or not the L:TL relationship remains isometric through ontogeny requires testing, but the ratio can be used to extrapolate rough TL measurements from L values of isolated mandibular tooth plates. For example, the L value of the holotype and SDNHM 25417 would suggest that the fish when alive measured about 172 and 99 cm TL, respectively, and the smallest and largest individuals represented by isolated mandibular plates of *I. bifurcatus* in

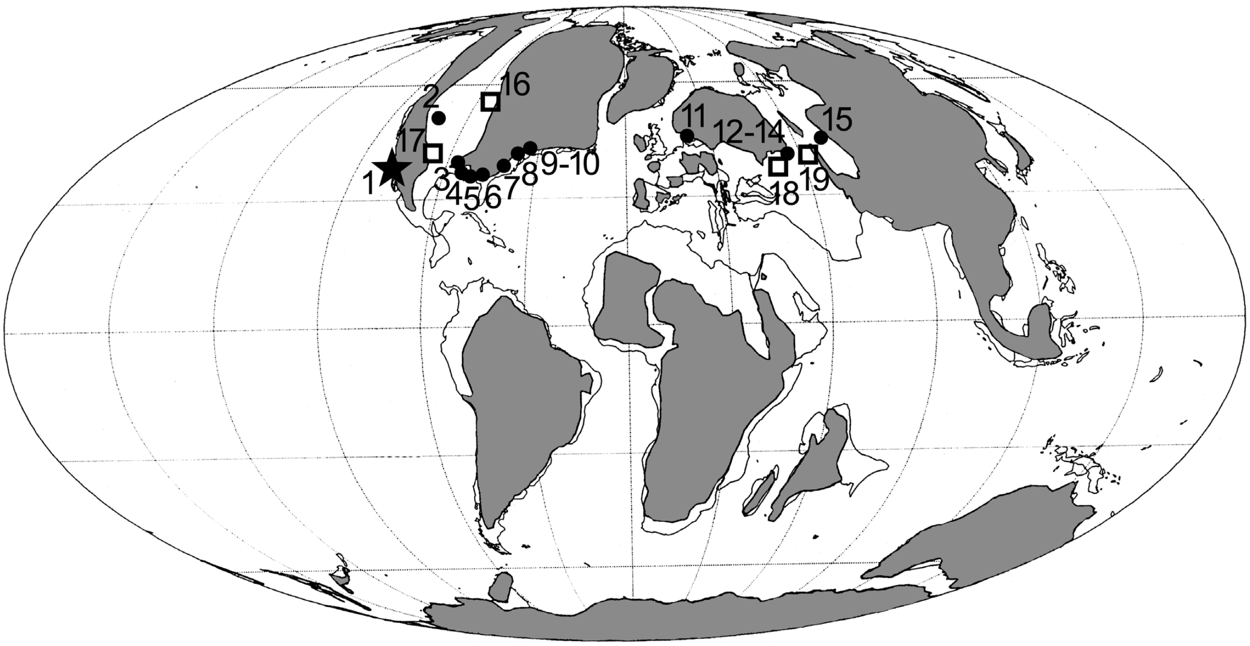

Figure 3. Campanian paleogeography (after Smith *et al.*, 1994, map 11) showing localities of *Ischyodus bifurcatus* and related species of the '*bifurcatus*-group' (plots and locality numbers based on Appendix 1). Symbols: star, *I. bifurcatus* from California described in the present study (SDNHM 25417: Figure 2); circles, all other *I. bifurcatus* records; squares, all other Late Cretaceous records of species of the '*bifurcatus*-group.'

the SSU collection suggest a *TL* range of 76 to 156 cm. Even if a conservative *L*:*TL* ratio as low as, for example, 1:18 is used, the holotype and SDNHM 25417 would have roughly measured at least about 1.5 and 0.8 m *TL*, respectively (see also Popov *et al.*, 2013).

In his original description of *Ischyodus bifurcatus*, Case (1978) listed occurrences of the species from Santonian to Maastrichtian deposits of the USA, including Delaware, New Jersey, and Arkansas (Figure 3; Appendix 1). Subsequently, additional North American occurrences were reported from Montana, Wyoming, Alabama, Georgia, and North Carolina (Case, 1979; Robb, 1989; Case and Schwimmer, 1992; Cicimurri and Ebersole, 2014). Elsewhere, *I. bifurcatus* is also known from the Campanian of Sweden (Davis, 1890; see above) and the Campanian–Maastrichtian of European Russia (e.g. Averianov and Popov, 1995, 2014; Nessov and Averianov, 1996; Popov, 2004; Appendix 1). Case (1978) and Case and Schwimmer (1992) also listed occurrences of *I. bifurcatus* from the lower Campanian of Chico, California, the middle Campanian of New Jersey, the upper Campanian of Belgium, the upper Campanian to lower Maastrichtian of New Mexico, and the upper Campanian of Belgium (Appendix 1). These records, however, are unverifiable because they are based on specimens in private collections and their taxonomic identity cannot be confirmed due to the lack of illustrations. Verified records of *I. bifurcatus* indicate that the species is confined to the mid-latitudinal zone in the Northern Hemisphere and has a temporal range of about 20 Ma (Santonian to Maastrichtian). SDNHM 25417 is significant because it constitutes the first confirmed record of *I. bifurcatus* from the North Pacific region (Figure 3). In addition, the present fossil record of *I. bifurcatus* (Figure 3; Appendix 1) suggests that this taxon first evolved in the region of the present-day eastern and southeastern United States during the late Santonian (i.e., Mississippi, Alabama, and Delaware records) and dispersed eastward as far as present-day northern Kazakhstan via the northern shoreline of the Tethys Sea during the late Maastrichtian, and westward as far as present-day southern California, likely via the southern shoreline of the Late Cretaceous 'Laramidia,' during the late Campanian (Appendix 1; Figure 3).

Ischyodus yanshini from the lower Campanian of western Kazakhstan is a species of the '*bifurcatus*-group' that is characterized by mandibular plates with a narrow median tritor and short anterior outer tritor (see Averianov, 1991). *Ischyodus yanshini* is considered to be closest phylogenetically to *I. bifurcatus* on the basis of their morphological resemblance. Based on isolated tooth plates from North Dakota, Colorado and Russia, Hoganson and Erickson (2005) erected a new Maastrichtian species of *Ischyodus*, *I. rayhaasi*, here included in the '*bifurcatus*-group' (see also Hoganson *et al.*, 2015). Mandibular plates of *I. rayhaasi* differ from those of *I. bifurcatus* by an unequally bifurcated median tritor with the tip of its outer branch lying directly posterior to the anterior outer tritor and with its inner branch extending beyond the anterior tip of the anterior outer tritor (Hoganson and Erickson, 2005). The presence of an 'indistinct accessory median tritor' on the mandibular plate diagnosed for this species in the original description is not unique to *I. rayhaasi* because a similar additional tritor is also present in the holotype of *I. bifurcatus* (see above). It should be noted that palatine and vomerine tooth plates among these '*bifurcatus*-group' species are less taxonomically diagnostic compared to their mandibular tooth plates (Popov, 2004; the vomerine tooth plate is unknown for *I. rayhaasi*). The present fossil record suggests that *I. bifurcatus* has the geologically oldest origin among the three '*bifurcatus*-group' species (i.e., *Ischyodus bifurcatus*, *I. rayhaasi*, and *I. yanshini*; Appendix 1). The geographic distribution of this group strongly indicates that the three species preferred shallow epicontinental seas and shelf environments of temperate latitudes in the Northern Hemisphere (Figure 3).

Other reports of chimaeroid fossils in the North Pacific include, in addition to SDNHM 25417, a dorsal fin spine of *Edaphodon* sp. from the lower Miocene of Kern County, California (Takeuchi and Huddleston, 2006), as well as numerous tooth plates of *Hydrolagus* cf. *colliei* (Lay and Bennett, 1839) and *Harriotta* cf. *raleighana* Goode and Bean, 1895, from the lower Miocene–early Pliocene at several localities in southern California (Popov and Takeuchi, 2011). Applegate (1975) reported a tooth plate of *Ischyodus zinsmeisteri* Applegate, 1975, from the Paleocene of Ventura County, California; however, this specimen is considered to belong to the genus *Edaphodon*, rather than *Ischyodus* (EVP, personal observation). An additional eastern North Pacific record comes from the lower Campanian of Vancouver Island, British Columbia, Canada, represented by *Edaphodon hesperis* Shin, 2010, based on an associated dentition (Shin, 2010). In contrast to the eastern North Pacific, the western North Pacific record of fossil chimaeroids is limited. Examples include an isolated mandibular tooth plate of *Edaphodon* sp. from the late Oligocene of Japan (Okazaki, 1991), and another such of *Chimaera* sp. from the middle Miocene of Japan (Nomura, 2000). In addition, Uyeno and Takahashi (1997) briefly noted an occurrence of an associated(?) specimen of *Ischyodus*(?) from the Upper Cretaceous (Coniacian) of Japan, consisting of two (vomerine and mandibular) tooth plates and a dorsal fin spine; however, the specimen has not yet been described formally and its exact taxonomic identity remains uncertain. The scarcity of chimaeroid fossil records in the region is at odds with the fact that numerous Cretaceous and Cenozoic deposits rich in teeth of fossil elasmobranchs are present in Japan (e.g. Yabumoto and Uyeno, 1994; Goto *et al.*, 1996) and chimaeroid materials commonly co-occur with elasmobranch remains elsewhere (e.g. Popov and Machalski, 2014). Such chimaeroid fossils may exist in museum and private collections in Japan, but the diversity and abundance, as well as stratigraphic and geographic distributions, of fossil chimaeroids in the western North Pacific remain poorly understood. Taking all these occurrence data into account, SDNHM 25417 is important because it constitutes the first known record of *I. bifurcatus* from the North Pacific region and it represents the only known definite Mesozoic record of the genus in the entire North Pacific region.

Conclusions

SDNHM 25417 is a nearly complete right mandibular tooth plate of *Ischyodus bifurcatus* that was collected from the upper Campanian portion of the Point Loma Formation in San Diego County, California, USA. It likely came from an individual that measured nearly 1 m *TL*. A review of occurrence records shows that *I. bifurcatus* geologically ranges for about 20 Ma from the Santonian to Maastrichtian. Specimens of *I. bifurcatus* occur in deposits formed in epicontinental seas and shelf paleoenvironments of temperate latitudes in the Northern Hemisphere. Published localities include Delaware, New Jersey, North Carolina, Georgia, Alabama, Arkansas, Montana, and Wyoming of the United States as well as Sweden and European Russia. SDNHM 25417 is significant because (1) it constitutes the first confirmed record of *I. bifurcatus* from the circum-Pacific, and (2) it represents the only known Mesozoic record of *Ischyodus* in the entire North Pacific region.

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References

Agassiz, L., 1833–1843 [1843]: *Recherches sur les Poissons Fossiles*, 1420 p. Imprimerie de Petitpierre, Neuchâtel.

Applegate, S. P., 1975: A new species of Paleocene chimaeroid from California. *Bulletin of the Southern California Academy of Sciences*, vol. 74, p. 27–30.

Averianov, A. O., 1991: A new species of chimaeroids of the genus *Ischyodus* from the Campanian of Western Kazakhstan. *Proceedings of the Kazakh SSR Academy of Sciences*, *Geological Series*, vol. 1, p. 32–34. (*in Russian; original title translated*)

Averianov, A. O. and Popov, E. V., 1995: A new species of chimaeroid fish from the Upper Cretaceous of the Saratov region, Russia. *Palaeontology*, vol. 38, p. 659–664.

Averianov, A. O. and Popov, E. V., 2014: A pterosaurian vertebra from the Upper Cretaceous of the Saratov Region. *Paleontological Journal*, vol. 48, p. 326–329.

Bishop, G. A., 1988: Two crabs, *Xandaros sternbergi* (Rathbun 1926) n. gen., and *Icriocarcinus xestos* n. gen., n. sp., from the Late Cretaceous of San Diego County, California, USA, and Baja California Norte, Mexico. *Transactions of the San Diego Society of Natural History*, vol. 21, p. 245–257.

Bonaparte, C. L., 1832: *Iconografia della Fauna Italica per le Quattro Classi degli Animali Vertebrati*. *Tomo III. Pesci*, 6 p. Dalla Tipografia Salviucci, Rome.

Buckland, W., 1835: A notice on the fossil beaks of four extinct species of fishes, referable to the genus *Chimaera*, which occur in the Oolitic and Cretaceous Formations of England. *Proceedings of the Geological Society of London*, vol. 2, p. 205–208.

Bukry, D., 1994: Coccolith correlation of Late Cretaceous Point Loma Formation at La Jolla and Carlsbad, San Diego County, California. *U. S. Geological Survey Open-file Report 94-678*, p. 1–23.

Case, G. R., 1967: *Fossil Shark and Fish Remains of North America*, 20 p. Private Publication, Ridgefield Park.

Case, G. R., 1978: *Ischyodus bifurcatus*, a new species of chimaeroid fish from the Upper Cretaceous of New Jersey. *Geobios*, vol. 11, p. 21–29.

Case, G. R., 1979: Additional fish records from the Judith River Formation (Campanian) of Montana. *Geobios*, vol. 12, p. 223–233.

Case, G. R. and Schwimmer, D. R., 1992: Occurrence of the chimaeroid *Ischyodus bifurcatus* Case in the Cussetta Formation (Upper Cretaceous, Campanian) of western Georgia and its distribution. *Journal of Paleontology*, vol. 66, p. 347–350.

Cicimurri, D. J. and Ebersole, J. A., 2014: Late Cretaceous chimaeroids (Chondrichthyes: Holocephali) from Alabama, USA. *PaleoBios*, vol. 31, p. 1–14.

Cicimurri, D. J. and Ebersole, J. A., 2015: Paleocene chimaeroid fishes (Chondrichthyes: Holocephali) from the eastern United States, including two new species of *Callorhinchus*. *PaleoBios*, vol. 32, p. 1–29.

Coombs, W. P. Jr. and Deméré, T. A., 1996: A Late Cretaceous nodosaurid ankylosaur (Dinosauria: Ornithischia) from marine sediments of coastal California. *Journal of Paleontology*, vol. 70, p. 311–326.

Davis, J. W., 1890: On the fossil fish of the Cretaceous formation of Scandinavia. *Scientific Transactions of the Royal Dublin Society*, vol. 2, p. 363–434.

Didier, D. A., Kemper, J. M. and Ebert, D. A., 2012: Phylogeny, biology, and classification of extant Holocephalans. *In*, Carrier, J. C., Musick, J. A. and Heithaus, M. R. *eds*., *Biology of Sharks and Their Relatives*, *Second Edition*, p. 97–122. CRC Press, Boca Raton.

Egerton, P. G., 1843: On some new species of fossil chimaeroid fishes, with remarks on their general affinities. *Proceedings of the Geological Society of London*, vol. 4, p. 153–157.

Ford, T. L. and Kirkland, J. I., 2001: Carlsbad ankylosaur (Ornithischia, Ankylosauria): an ankylosaurid and not a nodosaurid; *In*, Carpenter, K. *ed*., *The Armored Dinosaurs*, p. 239–260. Indiana University Press, Bloomington.

Garman, S., 1901: Genera and families of the chimaeroids. *Proceedings of the New England Zoological Club*, vol. 2, p. 75–77.

Goode, G. B. and Bean, T. H., 1895: Scientific results of explorations by the U.S. Fish Commission Steamer "*Albatross*". No. XXX. On *Harriotta*, a new type of chimaeroid fish from the deeper waters of the northwestern Atlantic. *Proceedings of the U.S. National Museum*, vol. 17, p. 471–473, pl. 19.

Goto, M., Uyeno, T. and Yabumoto, Y., 1996: Summary of Mesozoic elasmobranch remains from Japan. *In*, Arratia, G. and Viohl, G. *eds*., *Mesozoic Fishes I—Systematics and Paleoecology*, p. 73–82. Verlag Dr. Friedrich Pfeil, München.

Groves, L. T., 1990: New species of Late Cretaceous Cypraeacea (Mollusca: Gastropoda) from California and Mississippi, and a review of Cretaceous cypraeaceans of North America. *Veliger*, vol. 33, p. 272–285.

Hilton, R. P., 2003: *Dinosaurs and Other Mesozoic Reptiles of California*, 356 p. University of California Press, Berkeley.

Hoganson, J. W. and Erickson, J. M., 2005: A new species of *Ischyodus* (Chondrichthyes: Holocephali: Callorhynchidae) from Upper Maastrichtian shallow marine facies of the Fox Hills and Hell Creek formations, Williston Basin, North Dakota, USA. *Palaeontology*, vol. 48, p. 709–721.

Hoganson, J. W., Erickson, J. M. and Everhart, M. J., 2015: *Ischyodus rayhaasi* (Chimaeroidei; Callorhynchidae) from the Campanian–Maastrichtian Fox Hills Formation of northeastern Colorado, USA. *Transactions of the Kansas Academy of Science*, vol. 118, p. 27–40.

Huxley, T. H., 1880: *A Manual of the Anatomy of Vertebrated Animals*, 431 p. D. Appleton and Company, New York.

Lay, G. T. and Bennett, E. T., 1839: *Fishes. The Zoology of Captain Beechey's Voyage ... to the Pacific and Behring's Straits ... in 1825-28*, p. 41–75. H. G. Bohn, London.

Loch, J. D., 1989: A new genus of aporrhaid gastropod from southern California. *Journal of Paleontology*, vol. 63, p. 574–577.

Nelson, J. S., 2006: *Fishes of the World*, *Fourth Edition*, 601 p. John Wiley and Sons, Hoboken.

Nelson, J. S., Grande, T. C. and Wilson, M. V. H., 2012: *Fishes of the World*, *Fifth Edition*, 707 p. John Wiley and Sons, Hoboken.

Nessov, L. A., 1997: *Cretaceous Nonmarine Vertebrates of Northern Eurasia*, 218 p. Institute of the Earth's Crust, University of Saint Petersburg, Saint Petersburg. (*in Russian; original title translated*)

Nessov, L. A. and Averianov, A. O., 1996: Ancient chimaeriform fishes of Russia, Ukraine, Kazakhstan and Middle Asia. I. Some ecological characteristics of chimaeroids and a summary of their occurrences. *Bulletin of Saint-Petersburg University*, vol. 7, p. 11–19. (*in Russian with English summary*)

Newton, E. T., 1878: The chimaeroid fishes of the British Cretaceous rocks. *Memoirs of the Geological Survey of the United Kingdom*, vol. 4, p. 1–62.

Nomura, M., 2000: A left tooth plate on the lower jaw of *Chimaera* from the Middle Miocene Nanao Calcareous Sandstone, Nanao, Noto, central Japan. *Report of the Nanao Children Science Museum*, No. 4, p. 25–42. (*in Japanese*)

Obruchev, D. V., 1953: Studies on edestids and the works of A.P. Karpinski. *Transactions of the Palaeontological Institute of the Academy of Sciences of the USSR*, vol. 45. p. 1–86. (*in Russian; original title translated*)

Okazaki, Y., 1991: A fossil dental plate of chimaeroid (Pisces: Holocephali) from the Oligocene Ashiya Group, Kyushu, Japan. *Bulletin of the Kitakyushu Museum of Natural History*, vol. 10, 105–107. (*in Japanese with English abstract*)

Ørvig, T., 1985: Histologic studies of ostracoderms, placoderms and fossil elasmobranchs. 5. Ptyctodontid tooth plates and their bearing on holocephalan ancestry: the condition of chimaeroids. *Zoologica Scripta*, vol. 14, p. 55–79.

Owen, R., 1846: *Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals. Part 1. Fishes*, 304 p. Longman, Brown, Green, and Longmans, London.

Panteleyev, A. V., Popov, E. V. and Averianov, A. O., 2004: New record of *Hesperornis rossicus* (Aves, Hesperornithiformes) in the Campanian of Saratov Province, Russia. *Paleontological Research*, vol. 8, p. 115–122.

Patterson, C., 1965: The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London*, *Series B*, vol. 249, p. 101–219.

Patterson, C., 1992: Interpretation of the toothplates of chimaeroid fishes. *Zoological Journal of the Linnean Society*, vol. 106, p. 33–61.

Popov, E. V., 1999: New data on tooth plate morphology of chimaeroid fishes of the genus *Ischyodus* from the Cretaceous and Paleogene of Central Russia and Volga Region. *In*, Darevskii, I. S. and Averianov, A. O. *eds*., *Materials on the History of Fauna of Eurasia*, p. 67–82. Proceedings of the Zoological Institute of the Russian Academy of Sciences, vol. 277, ZIN RAS, Saint Petersburg. (*in Russian with English summary*)

Popov, E. V., 2003: A new genus of elephant fishes (Holocephali: Callorhinchidae) from the Upper Callovian of the Volga Region near Saratov, Russia. *Paleontological Journal*, vol. 37, p. 507–513.

Popov, E. V., 2004: *Cretaceous and Paleocene Chimaeroid Fishes (Holocephali, Chimaeroidei) from the South of European Russia (Morphology, Systematics, Stratigraphical Distribution)*, 430 p. Ph.D. Thesis. Saratov State University, Saratov. (*in Russian; original title translated*)

Popov, E. V. and Beznosov, P. A., 2006: Remains of chimaeroid fishes (Holocephali: Chimaeroidei) from the Upper Jurassic deposits of Komi Republic, Russia. *In*, Rozanov, A. Y., Lopatin, A. V. and Parkhaev, P. Y. *eds.*, *Modern Russian Paleontology: Classic and Newest Methods—2006*, p. 55–64. Russian Academy of Sciences, Paleontological Institute, Moscow. (*in Russian with English summary*)

Popov, E. V., Duffin, C. J., Tischlinger, H. and Atuchin, A., 2013: Reconstructions of the German Plattenkalk (Late Jurassic) chimaeroid fishes (Holocephali, Chimaeroidei). *In*, Schwarz, C. and Kriwet, J. *eds*., *Sixth International Meeting on Mesozoic Fishes: Diversification and Diversity Patterns. Abstracts*, p. 56. Verlag Friedrich Pfeil, Munich.

Popov, E. V. and Efimov, V. M., 2012: New records of the chimaeroid genus *Stoilodon* Nessov et Averianov, 1996 (Holocephali, Chimaeroidei) remains from the Late Jurassic and Early Cretaceous of European Russia. *Proceedings of Saratov University*, *Earth Sciences*, vol. 12, p. 66–79. (*in Russian with English abstract*)

Popov, E. V. and Ivanov, A. V., 1996: 'Oscillating tendencies' in morphogenesis in the Cretaceous–Paleogene *Ischyodus* (Chimaeroidei, Edaphodontidae). *In*, Zayontz, V. N. and Ivanov, A. V. *eds*., *Collection of Papers of the Conference 'Geological Sciences, 96'*, p. 53–57. Saratov State University, Saratov. (*in Russian; original title translated*)

Popov, E. V. and Machalski, M., 2014: Late Albian chimaeroid fishes (Holocephali, Chimaeroidei) from Annopol, Poland. *Cretaceous Research*, vol. 47, p. 1–18.

Popov, E. V. and Takeuchi, G., 2011: Miocene–early Pliocene chimaeroid fishes (Holocephali, Chimaeroidei) from California and a review of the global Neogene chimaeroid diversity and distribution. *Journal of the Vertebrate Paleontology*, *Program and Abstracts*, *2011*, p. 175.

Popov, E. V. and Yarkov, A. A., 2001: A new giant species of *Edaphodon* (Holocepali: Edaphodontidae) from the Beryozovaya Beds (Lower Paleocene) of the Volgograd Volga Region. *Paleontological Journal*, vol. 35, p. 183–187.

Robb, A. J., III, 1989: The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen Country, North Carolina. *Mosasaur*, vol. 4, p. 75–92.

Shin, J.-Y., 2010: A new species of *Edaphodon* (Chondrichthyes: Holocephali) from the Upper Cretaceous Haslam Formation, Vancouver Island, British Columbia, Canada. *Journal of Vertebrate Paleontology*, vol. 30, p. 1012–1018.

Sliter, W. V., 1968: Upper Cretaceous Foraminifera from southern California and northwestern Baja California, Mexico. *University of Kansas Paleontological Contributions*, no. 49, p. 1–141.

Smith, A. G., Smith, D. G. and Funnell, B. M., 1994: *Atlas of Mesozoic and Cenozoic Coastlines*, 99 p. Cambridge University Press, Cambridge.

Squires, R. L. and Saul, L. R., 2001: New Late Cretaceous gastropods from the Pacific slope of North America. *Journal of Paleontology*, vol. 75, p. 46–65.

Stahl, B. J., 1999: Chondrichthyes III—Holocephali. *In*, Schultze, H.-P. *ed*., *Handbook of Paleoichthyology*, vol. 4, p. 1–164. Verlag Friedrich Pfeil, Munich.

Takeuchi, G. T. and Huddleston, R. W., 2006: A Miocene chimaeroid fin spine from Kern County, California. *Bulletin of the Southern California Academy of Sciences*, vol. 105, p. 85–90.

Uyeno, T. and Takahashi, M., 1997: Chimaeroid fish yielded from the Upper Cretaceous Futaba Formation in Iwaki City, Japan. *Abstracts with Programs*, *1997 Annual Meeting of the Palaeontological Society of Japan*, *Kyoto*, p. 165. (*in Japanese*)

Weigmann, S., 2016: Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *Journal of Fish Biology*, vol. 88, p. 837–1037.

Yabumoto, Y. and Uyeno, T., 1994: Late Mesozoic and Cenozoic fish faunas of Japan. *Island Arc*, vol. 3, p. 255–269.

Yarkov, A. A., 2001: New data on stratigraphy and fauna of the Upper Cretaceous deposits near Malaya Serdoba village (Penza Region). *Transactions of the Scientific-Research Geological Institute of the N. G. Chernyshevskii Saratov State University*, *New Series*, vol. 8, p. 55–61. (*in Russian with English abstract*)

Zverkov, N. G., Averianov, A. O. and Popov, E. V., 2017: Basicranium of an elasmosaurid plesiosaur from the Campanian of European Russia. *Alcheringa*, p. 1–15, doi: 10.1080/03115518.2017.1302508.

Author Contributions

E. D. J.-R. initiated and carried out this study. E. V. P. is primarily responsible for the taxonomic and technical aspects. T. A. D. supplied relevant geographic and stratigraphic contextual data of the specimen examined. K. S. oversaw the entire project and supplemented additional geological and paleontological information and literature. All authors contributed to the writing of the paper.

Appendix 1. Records of Late Cretaceous *Ischyodus bifurcatus* and related species of the '*bifurcatus*-group' with relevant references or referable specimens, including the Californian record described in this study. Numbered occurrences correspond to localities plotted in Figure 3; asterisk (*) indicates unverifiable record.

***Ischyodus bifurcatus* Case, 1978**

1. Point Loma Formation (upper Campanian), Carlsbad, California, USA (this study)
2. Mesaverde Formation (upper Campanian), Worland, Wyoming, USA (Case and Schwimmer, 1992)
3. Marlbrook Marl (upper Campanian), Arkadelphia, Arkansas, USA (Case, 1978)
4. Eutaw Formation (upper Santonian), Columbus, Mississippi, USA (Case and Schwimmer, 1992)
5. Mooreville Chalk (uppermost Santonian–mid-Campanian), Alabama, USA (Cicimurri and Ebersole, 2014, 2015)
6. Cassetta Formation (basal portion; mid-Campanian), Hannahatchee Creek, Georgia, USA (Case and Schwimmer, 1992, fig. 2)
7. Black Creek Formation (upper Campanian), Phoebus Landing, North Carolina, USA (Robb, 1989, fig. 13; referred to as *Ischyodus* cf. *bifurcatus*)
8. Merchantville Formation (upper Santonian–lower Campanian), St. Georges, Delaware, USA (Case, 1978)
9. Mount Laurel Sandstone (lower Maastrichtian), Monmouth County, New Jersey, USA (Case, 1978)
10. Navesink Formation (derived; lower–middle Maastrichtian), Monmouth County, New Jersey, USA (Case, 1978)
11. 'Campanian', Sweden (Davis, 1890; referred to as *Ischyodus brevirostris*)
12. Rybushka Formation (lower Campanian), numerous localities, Saratov region, Russia (Averianov and Popov, 1995, 2014; Panteleyev *et al*., 2004; Zverkov *et al*., 2017; SSU 154/108, 143, and 144)
13. Rybushka Formation (lower Campanian), several localities, Volgograd region, Russia (Nessov and Averianov, 1996; SSU 154/651 and 652)
14. Pudovkino Formation (upper Campanian), several localities, Penza Region, Russia (Yarkov, 2001; SSU 154/653 and 654)
15. Zhuravlev Formation (base; lower–upper Maastrichtian), Kushmurun, Kostanai Province, northern Kazakhstan (Nessov and Averianov, 1996, p. 16; SSU 154/655 and 656)

*Chico Fauna (lower Campanian), Chico, California, USA (Case, 1978)

*Woodbury Clay (mid-Campanian), Belmawr, New Jersey, USA (Case, 1978)

*Oburg Chalk (base, Cm2a; upper Campanian), Havre, Belgium (Case, 1978)

*Fruitland Formation (upper Campanian–lower Maastrichtian), San Juan Basin, New Mexico, USA (Case and Schwimmer, 1992)

*Zhuravlev Formation (base; upper Maastrichtian), Zhuravlevskyi, Kostanai region, northern Kazakhstan (Nessov and Averianov, 1996, p. 16)

***Ischyodus rayhaasi* Hoganson and Erickson, 2005**

16. Fox Hill Formation and Hell Creek Formation (Breien Member; upper Maastrichtian), numerous localities, North Dakota, USA (Hoganson and Erickson, 2005)
17. Fox Hill Formation (Campanian–Maastrichtian), Poison Springs Locality, Colorado, USA (Hoganson *et al*., 2015)
18. Berezovaya Beds (base; Danian, Paleocene; reworked from Bereslavka Formation; upper? Maastrichtian), Rasstrygin, Volgograd region, Russia (Popov and Ivanov, 1996; Popov and Yarkov, 2001; referred to as *Ischyodus bifurcatus*? or *I.* '*bifurcatus*')

***Ischyodus yanshini* Averianov, 1991**

19. Zhurun Beds (lower Campanian), Actobe region, western Kazakhstan (Averianov, 1991)

*'Lower Campanian,' Tykbytak, Actobe region, western Kazakhstan (Nessov and Averianov, 1996, p. 16; referred to as *Ischyodus* cf. *yanshini*)