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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

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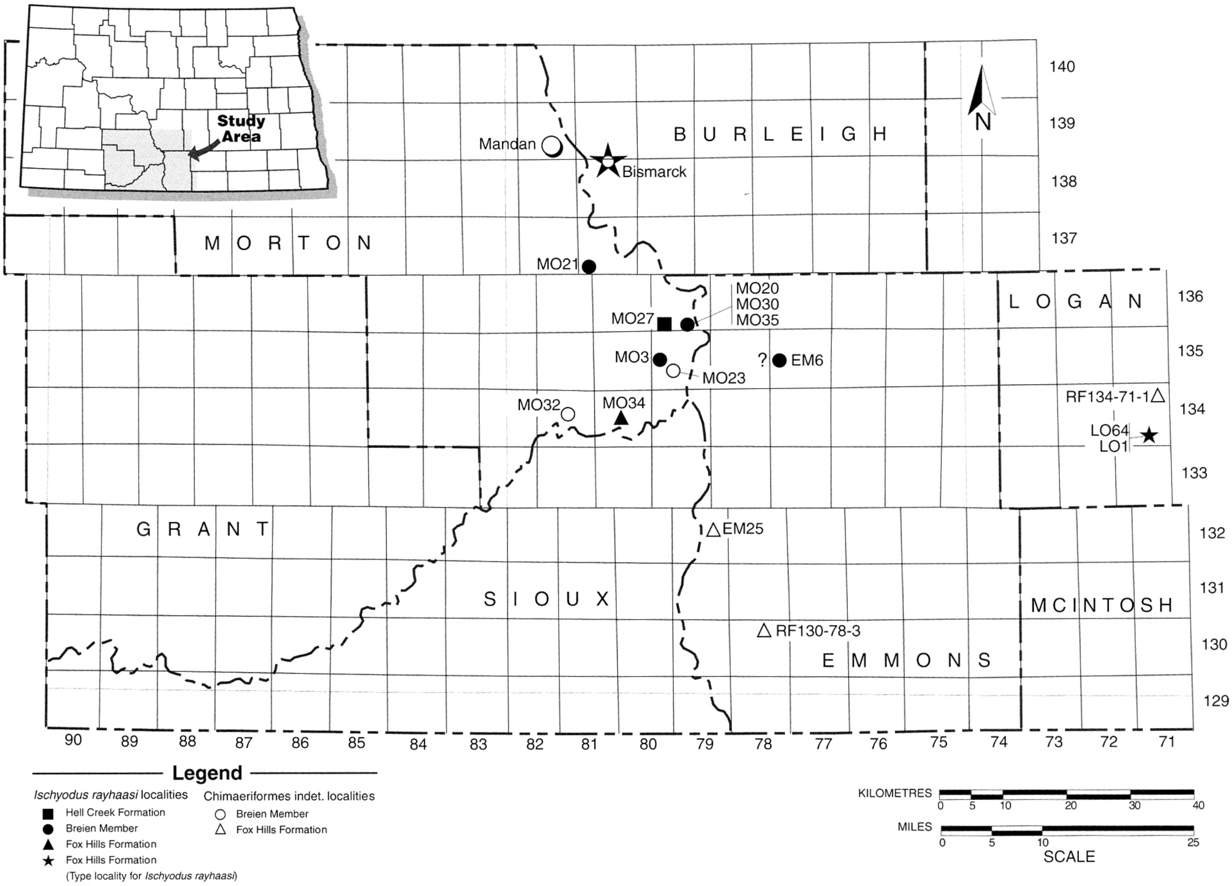
Abstract: A new species of chimaeroid, *Ischyodus rayhaasi* sp. nov., is described based primarily upon the number and configuration of tritors on palatine and mandibular tooth plates. This new species is named in honour of Mr Raymond Haas. Fossils of *I. rayhaasi* have been recovered from the Upper Maastrichtian Fox Hills Formation and the Breien Member and an unnamed member of the Hell Creek Formation at sites in south-central North Dakota and north-central South Dakota, USA. *Ischyodus rayhaasi* inhabited shallow marine waters in the central part of the Western Interior Seaway during the latest Cretaceous. Apparently it was also present in similar habitats at that time in the Volga region of Russia. *Ischyodus rayhaasi* is the youngest Cretaceous species of *Ischyodus* known to exist before the Cretaceous/Tertiary extinction, and the species apparently did not survive that event. It was replaced by *Ischyodus dolloi*, which is found in the Paleocene Cannonball Formation of the Williston Basin region of North Dakota and is widely distributed elsewhere.

Key words: *Ischyodus rayhaasi*, Holocephali, Maastrichtian, Fox Hills, Hell Creek, Breien, North Dakota.

DURING the course of larger studies of the stratigraphy and palaeontology of the Late Cretaceous (Maastrichtian) Fox Hills and Hell Creek formations in North Dakota, we found specimens of a new species of chimaeroid fish among a significant chondrichthyan fauna (Hoganson *et al.* 1994*a*, *b*, 1996; Hoganson and Murphy 2002). These strata represent deposition in the marine-to-delta platform transitional setting of the retreating Fox Hills Sea as it was invaded by the prograding Hell Creek (Sheridan) delta (Gill and Cobban 1973). Because of this dynamic setting, stratigraphic relationships are complicated by repeated facies changes that make documentation of fossils with potential biostratigraphic utility an important aspect of research in these rocks. Improved knowledge of Maastrichtian marine faunas in the midcontinent of North America is essential for accurate interpretation of regional palaeogeography (Erickson 1978, 1999) and biostratigraphy (Murphy *et al.* 1995; Hoganson and Murphy 2002), as well as for clarification of patterns of extinction and origination, particularly in proximity to the Cretaceous/Tertiary (K/T) boundary (Cvancara and Hoganson 1993; Hoganson *et al.* 1996, 1997; Hoganson 2000; Hoganson and Murphy 2002). Increased study of Maastrichtian faunas globally is advancing knowledge of the chimaeroids (e.g. Ward 1973; Case 1978; Ward and Grande 1991; Popov 1996; Popov and Ivanov 1996; Stahl 1999; Stahl and Chatterjee 1999, 2002; Duffin 2001). By describing this new chimaeroid species, we hope to contribute to the several areas of interest noted above.

LOCATION AND STRATIGRAPHIC SETTING

Over several field seasons, we have examined detailed stratigraphic relationships within and between formations of the Late Cretaceous regressive sequence, particularly the Fox Hills and Hell Creek formations, in the Missouri Valley region of south-central North Dakota. Vertebrate fossils are not abundant in these formations,



TEXT-FIG. 1. Map of North Dakota showing location of fossil sites where *Ischyodus rayhaasi* sp. nov. and other Chimaeriformes remains have been collected. Site numbers refer to North Dakota State Fossil Collection (NDSFC) fossil localities.

but specimens of a new callorhynchid species, here named *Ischyodus rayhaasi* sp. nov., have been discovered at three localities in the Fox Hills Formation and seven sites in the Hell Creek Formation (Text-figs 1–2; Table 1). These fossil sites are in Morton, Emmons and Logan counties, North Dakota.

Depositional setting and stratigraphic relationships are of importance to interpretations of the palaeoecology of this species. The regressive sequence of the Fox Hills–Hell Creek formations overlies offshore deposits of the Pierre Shale, an extensive Campanian and Early Maastrichtian formation in the central part of the Western Interior Seaway (WIS). Four members that document successively shallower marine conditions are recognized in the Fox Hills Formation (Waage 1968; Klett and Erickson 1977). Overlying the Pierre Shale are silty shale and sandy siltstone beds of the Trail City Member that contain a rich molluscan fauna deposited within the Maastrichtian *Hoploscaphites nicolletii* (ammonite) Zone (Kennedy *et al.* 1998) (Text-fig. 2). Trail City deposits represent sedimentation below wave base on the Fox Hills shelf. These deposits grade upward into shoreface, intertidal and barrier bar sandstone facies represented by the Timber Lake Member, which contains a diverse fauna. Deposited in a barrier island setting, the *in situ* fauna is a marine molluscan assemblage, but near the top of the member, a transported, mixed marine and brackish assemblage, which includes a sparse terrestrial vertebrate fauna and the ubiquitous trace fossil, *Ophiomorpha major* (Lesquereux, 1873), is present. The Timber Lake Member is within the *Jeletzkytes nebrascensis* (ammonite) Zone (Kennedy *et al.* 1998). Though never abundant, chondrichthyan teeth occur in both the marine and the mixed assemblages of the Timber Lake Member (Hoganson *et al.* 1994*a*, *b*, 1996).

Abruptly overlying the Timber Lake Member are lagoonal siltstone and claystone interlaminated on a centimetre scale, which Waage (1968) termed the Bullhead lithofacies. These rocks are truncated by tidal channel deposits consisting of muddy sandstone with erosional bases, the Colgate lithofacies of Waage (1968). Together these two lithofacies comprise the Iron Lightning Member of the Fox Hills Formation (Waage 1968; Erickson 1992), which contains a brackish water fauna dominated by the

TABLE 1. Chimaeriformes specimens from the Fox Hills Formation, Hell Creek Formation, and Breien Member of the Hell Creek Formation. NDSFC numbers are specimen numbers of the North Dakota State Fossil Collection, North Dakota Heritage Center, Bismarck. Locality numbers are North Dakota State Fossil Collection fossil site numbers. ^, partial specimen; *, estimate; NM, not measured.

Taxon	NDSFC specimen no.	Element	Formation/ Member	Measurement (mm)	Location
Ischyodus rayhaasi	ND 99-6.1 (Pl. 1, figs 10–12)	Lt. mandible (holotype)	Fox Hills	length, 64·39 width, 29·38 thick, 13·13	LO64
	ND 95-13.32 (Pl. 1, figs 1–2)	Rt. palatine (paratype)	Fox Hills	length, 25·68 width, 14·65 thick, 7·61*	LO1
	ND 00-58.1 (Pl. 1, figs 3–4)	Rt. palatine (paratype)	Fox Hills	length, 30·02 width, 15·38 thick, 14·03*	MO34
	ND 93-1.1 (Pl. 1, fig. 9)	Rt. palatine (paratype)	Hell Creek	length, 23·22 width, 12·83 thick, 8·75*	MO27
	ND 95-15.1 (Pl. 1, figs 5–7)	Rt. palatine (paratype)	Hell Creek/ Breien Mbr	length, 25·73 width, 11·88 thick, 7·38	MO20
	ND 99-12.1 (Pl. 1, fig. 8)	Lt. palatine^ (paratype)	Hell Creek/ Breien Mbr	length, 23·36 width, 12·52 thick, 9·39*	MO3
	ND 00-37.1	Lt. mandible	Hell Creek/ Breien Mbr	length, 33·88 width, 24·66 thick, 7·82	MO30
	ND 95-15.3	Rt. palatine^	Hell Creek/ Breien Mbr	length, 28·90* width, 15·05* thick, 7·72	MO20
	ND 95-15·8	Rt. mandible^	Hell Creek/ Breien Mbr	length, 26·40* width, 14·40* thick, 6·25	MO20
	ND 350.1	Rt. mandible^	Hell Creek/ Breien Mbr	length, 34·92* width, 19·07* thick, 7·44*	MO21
Ischyodus cf. *I. rayhaasi*	ND 95-15.2	Rt. mandible^	Hell Creek/ Breien Mbr	NM	MO20
	ND 99-23.1	Lt. mandible^	Hell Creek/ Breien Mbr	NM	EM6
Ischyodus sp.	ND 95-15.4	Rt. palatine^	Hell Creek/ Breien Mbr	NM	MO20
	ND 95-15.5	Lt. palatine^	Hell Creek/ Breien Mbr	NM	MO20
	ND 95-15.6	Lt. palatine^	Hell Creek/ Breien Mbr	NM	MO20
	ND 95-15.7	Lt. palatine^	Hell Creek/ Breien Mbr	NM	MO20
Chimaeriformes indet.	ND 95-13	2 fragments	Fox Hills	NM	LO1
	ND 99-6	2 fragments	Fox Hills	NM	LO64
	ND 99-6	2 fragments	Fox Hills	NM	LO64
	ND 95-5	1 fragment	Fox Hills	NM	EM25
	ND 00-40	1 fragment	Hell Creek/ Breien Mbr	NM	MO32
	ND 00-59	1 fragment	Hell Creek/ Breien Mbr	NM	MO35

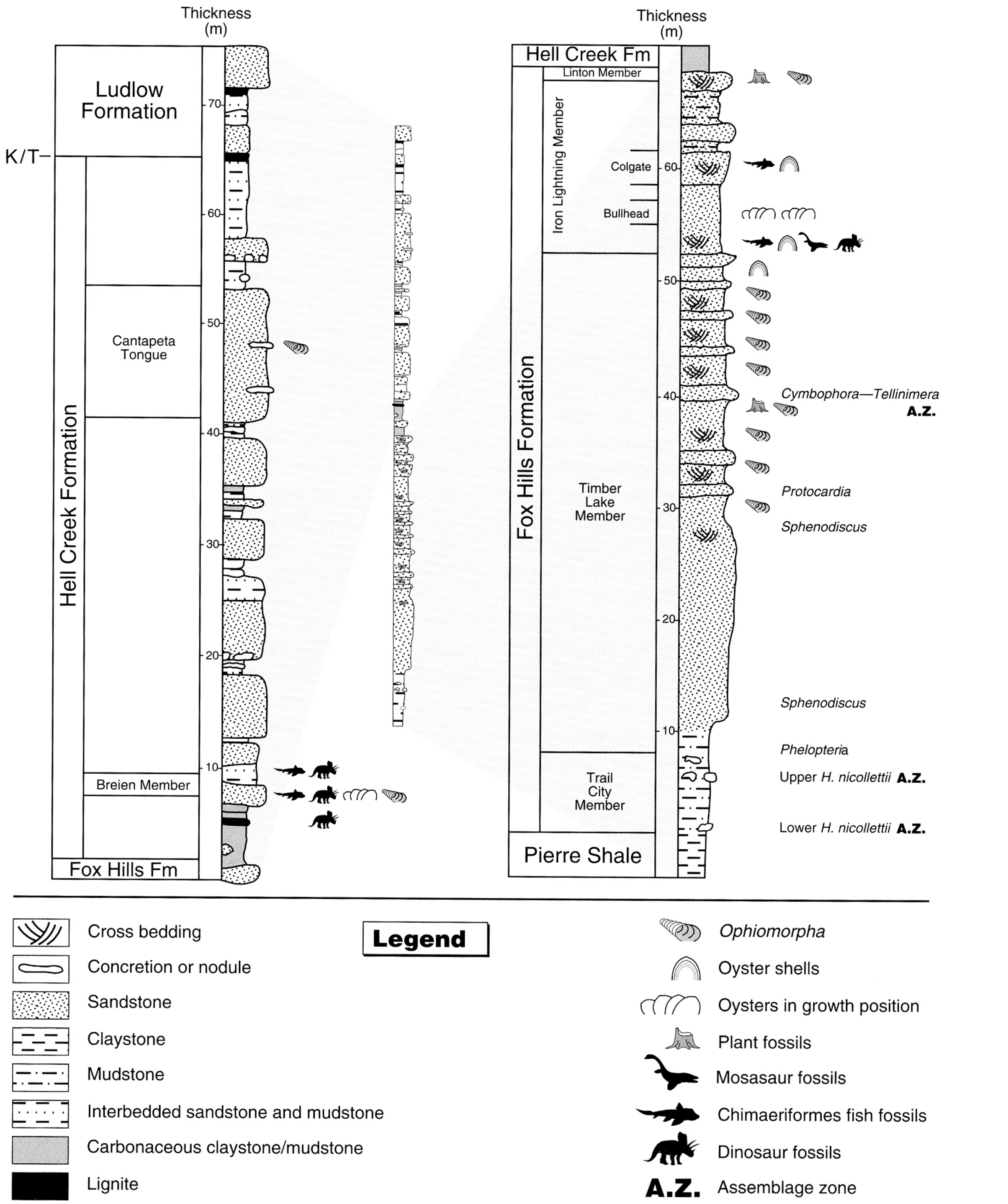
TABLE 1. Continued

Taxon	NDSFC specimen no.	Element	Formation/ Member	Measurement (mm)	Location
	ND 96-4	10 fragments	Hell Creek/ Breien Mbr	NM	MO27
	ND 99-113	1 fragment	Hell Creek/ Breien Mbr	NM	MO23
	ND 95-15	19 fragments	Hell Creek/ Breien Mbr	NM	MO20
	RF130-78-3 R. M. Feldmann loc. Sec. 3, T130N, R78W Emmons Co., ND	1 fragment	Fox Hills	NM	
	RF134-71-1 R. M. Feldmann loc. Sec. 1, T134N, R71W Logan Co., ND	1 fragment	Fox Hills	NM	
	JE21-24-14 S½, SE1/4, Sec. 14, T21N, R24E Corson Co., SD	2 fragments	Fox Hills	NM	
Mylognathus priscus	Waage, 1968 Loc. 74 Moreau R. Valley Ziebach Co., SD	Rt. mandible 1 fragment	Fox Hills/Iron Lightning Mbr	NM	
Mylognathus priscus	Feldmann and Palubniak, 1975 NE1/4, SE1/4, Sec. 11 and NW1/4, SW1/4, Sec. 12, T. 132 N, R. 79 W, Emmons Co., ND	Rt. mandible	Fox Hills/Timber Lake Mbr	NM	

oyster *Crassostrea subtrigonalis* (Evans and Shumard, 1857), often found in life position in the Bullhead lithofacies. The base of the Iron Lightning Member often occurs at a tidal channel, or storm-eroded, lag deposit developed upon sandstone of the Timber Lake Member. Such lags produce the mixed marine, brackish and terrestrial fauna generally dominated by worn valves of *C. subtrigonalis*, but also containing chondrichthyan teeth, including chimaeroids, beanid turtle scutes, and mosasaur and crocodile teeth (Hoganson *et al.* 1994*a*, *b*). These lag deposits have been included in the Timber Lake Member by some workers (Feldmann and Palubniak 1975), although Erickson (1974) has suggested they are more appropriately related to post-Timber Lake depositional events and facies. Stratigraphic relationships at most Fox Hills sites are difficult to determine due to incomplete sections, yet concentrations of transported (abraded) *C. subtrigonalis* usually indicate lag-type depositional settings on an erosional surface with proximity to both terrestrial and marine habitats.

Their presence on erosional surfaces, or in mixed faunal assemblages, typifies chimaeroid finds reported herein and also explains the impressions of stratigraphic assignment of some sites indicated on Text-figure 2. Facies patterns become more complicated to the south-east where the land bridge of the Dakota Isthmus began to form (Erickson 1978, 1999). A delta plain represented by freshwater and terrestrial sandstone, siltstone and shale of the Hell Creek Formation produced this palaeogeographical configuration, which was locally re-invaded by marine waters on several occasions. A 5–10-m-thick, estuarine, medium- to coarse-grained, well-indurated sandstone, termed the Linton Member (Klett and Erickson 1977), represents the last Fox Hills deposit before the Hell Creek deltaic system dominated the region. Fossils in the Linton Member include *Ophiomorpha*, the limulid *Casterolimulus kletti* Holland, Erickson and O'Brien, 1975, petrified wood, and a suite of plants that reflect subtropical to warm temperate oceanic coastal conditions. Intertonguing relationships with the Hell Creek Formation are implied by the flora (Peppe and Erickson 2002). An intervening palaeosol or thin lignite bed marks the formational contact between the Fox Hills and Hell Creek formations in several places in North Dakota but that organic-rich unit is not readily defined where estuary deposits of the Linton Member occur.

The last well-documented advance of the Fox Hills Sea onto the delta platform is represented by the Breien Member of the Hell Creek Formation (Laird and Mitchell 1942; Seager *et al.* 1942; Frye 1964, 1967, 1969; Hoganson and Murphy 2002; Murphy *et al.* 2002) although the Cantapeta Tongue in the upper part of the Hell Creek



TEXT-FIG. 2. Upper Cretaceous and the lower part of the Paleocene (Ludlow Formation) generalized stratigraphic section in North Dakota showing stratigraphic occurrence of Chimaeriformes fossils and lithologies from which they were collected.

Formation suggests a brief return to marine conditions (Murphy *et al.* 2002). The Breien Member consists of glauconitic sandstone and mudstone and occurs 1·5–9·0 m above the Fox Hills–Hell Creek formational contact (Hoganson and Murphy 2002) (Text-fig. 2). *Ophiomorpha*, other burrows and *Crassostrea subtrigonalis* commonly occur in this member. Other fossils are not common in the Breien Member, and its fossil assemblages generally consist of a mix of marine, brackish and terrestrial taxa including molluscs, fish, crocodylians, dinosaurs and mammals (Hoganson and Murphy 2002). The most abundant fossils are chondrichthyan teeth, including chimaeroid tooth plates (Hoganson and Murphy 2002). The Breien Member was deposited during or after the Late Maastrichtian *Jeletzkytes nebrascensis* (ammonite) Zone in shallow, nearshore, marine environments similar to those of the Fox Hills Formation.

COLLECTING AND LABORATORY METHODS

Field studies of the Hell Creek and Fox Hills formations aimed at faunal analysis and palaeobiogeographical and palaeoecological interpretation have been conducted in south-central North Dakota by us for more than 25 years. Rare chimaeroid fossils, tooth plates or fragments of tooth plates, have been recovered on occasion during that time from these formations. Most fossils were found as gleanings in lag deposits during surface prospecting. The *Ischyodus rayhaasi* holotype (ND 99-6.1) (Pl. 1, figs 10–12; Text-fig. 3), a nearly complete left mandibular tooth plate, was collected *in situ* from a Fox Hills Formation tidal channel deposit during excavation at locality LO64 (Text-fig. 2). Other chimaeroid specimens were recovered by screen washing at that site. No articulated skeletons or paired dental elements were found. Table 1 lists the locations where chimaeroid specimens were discovered, the type of dental element found and the taxonomic assignments of the elements. The list includes the specimen (ND 00-58.1) collected by Mr Raymond Haas from the Fox Hills Formation at locality MO34 that we have designated as a paratype of *Ischyodus rayhaasi*.

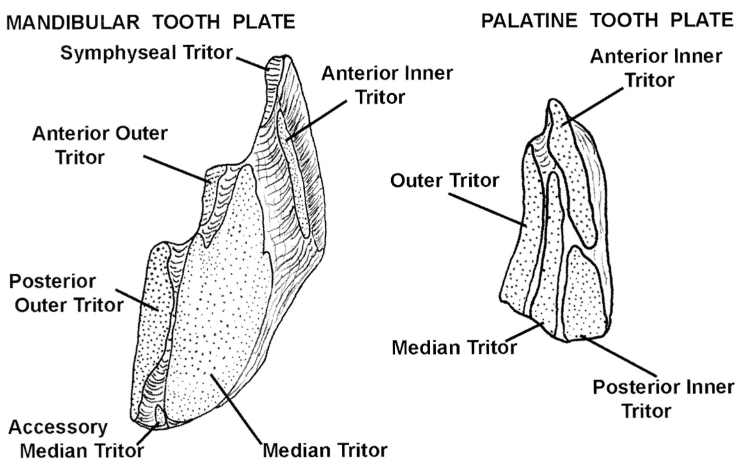
The only chimaeroid specimen previously illustrated from the Fox Hills Formation in North Dakota was collected as part of a bulk sample by D. S. Palubniak during a study of the palaeoecology of oyster assemblages. The specimen was illustrated and identified as *Mylognathus priscus* (Leidy) by Feldmann and Palubniak (1975, pl. 2, fig. 12). We believe that fossil is *Ischyodus rayhaasi* based on the illustration, although confirmation of the identity of the specimen is prevented because its whereabouts is unknown (R. M. Feldmann, pers. comm. 1998). Waage (1968, pl. 12, fig. M) also illustrated two chimaeroid specimens from the Fox Hills Formation in South Dakota and referred to them as *Mylognathus priscus*. We also believe that these are *I. rayhaasi* although we have not examined the specimens.

A chimaeroid palatine tooth plate (ND 95-15.1) (Pl. 1, figs 5–7; Text-fig. 3) from the Breien Member of the Hell Creek Formation in North Dakota (Table 1, locality MO) was illustrated and identified as *Ischyodus* sp. by Murphy *et al.* (1995, appendix E, fig. S). This same specimen was referred to as *Ischyodus* sp. nov. and illustrated by Hoganson and Murphy (2002, fig. 12E). We are designating this specimen as a paratype of *Ischyodus rayhaasi*.

Morphological terminology and tritoral nomenclature used in the fossil descriptions and in Text-figure 3 are adapted from Ward and Grande (1991) and Stahl (1999).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass SUBTERBRANCHIALIA Zangerl, 1979
Superorder HOLOCEPHALI Bonaparte, 1832
Order CHIMAERIFORMES Obruchev, 1953
Suborder CHIMAEROIDEI Patterson, 1965



TEXT-FIG. 3. Diagram of mandibular and palatine tooth plates of *Ischyodus rayhaasi* indicating the terminology used for tritors. Terminology adapted from Ward and Grande (1991) and Stahl (1999). Mandibular tooth plate diagram is based on the *Ischyodus rayhaasi* holotype (Pl. 1, figs 10–12) (ND 99-6.1) and the palatine tooth plate diagram is based on an *Ischyodus rayhaasi* paratype (Pl. 1, figs 5–7) (ND 95-15.1).

Family CALLORHYNCHIDAE Garman, 1901

Genus ISCHYODUS Egerton, 1843

Type species. Ischyodus townsendi (Buckland, 1835), from the Jurassic Great Oolite, Stonesfield, England.

Ischyodus rayhaasi sp. nov.

Plate 1, figures 1–12; Text-figure 3

1968 *Mylognathus priscus* (Leidy); Waage, pl. 12, fig. M.
1975 *Mylognathus priscus* (Leidy); Feldmann and Palubniak, p. 230, pl. 2, fig. 12.
1994 *Ischyodus* sp.; Hoganson, Campbell and Murphy, p. 95.
1995 *Ischyodus* sp.; Murphy, Nichols, Hoganson and Forsman, p. 66; p. 73, appendix D, fig. S.
1996 *Ischyodus ?bifurcatus*; Popov and Ivanov, p. 55, fig. 2.
1996 *Ischyodus*; Hoganson, Erickson and Holland, p. 41A.
1997 *Ischyodus*; Hoganson, Erickson, Cvancara and Holland, p. 53A.
2002 *Ischyodus* n. sp.; Hoganson and Murphy, p. 263, fig. 12E.

Derivation of name. Ischyodus rayhaasi is named in honour of Raymond Haas from Annapolis, Maryland, USA, longtime observer of Fox Hills and Hell Creek Formation vertebrates.

Type specimens. Holotype: left mandibular tooth plate, ND 99-6.1; Plate 1, figures 10–12; Text-figure 3. Paratypes: right palatine tooth plate, ND 95-13.32; Plate 1, figures 1–2; right palatine tooth plate, ND 00-58.1; Plate 1, figures 3–4; right palatine tooth plate, ND 95-15.1; Plate 1, figures 5–7; Text-figure 3; left palatine tooth plate, ND 99-12.1; Plate 1, figure 8; right palatine tooth plate, ND 93-1.1; Plate 1, figure 9.

Material. Twenty-eight chimaeriform specimens were collected from the Upper Fox Hills Formation, and from the Breien Member and undefined units of the Hell Creek Formation in North Dakota for this study. Ten specimens were assignable to *Ischyodus rayhaasi*. Because of incomplete preservation, two specimens were provisionally assignable to *Ischyodus rayhaasi*, four were only identified as *Ischyodus* sp. and 11 could only be recognized as Chimaeriformes indeterminate. None of these specimens presented morphologies inconsistent with *I. rayhaasi* and therefore we assume *I. rayhaasi* is the only species present. See Table 1 for specimen numbers, collection localities and measurements. Specimens are deposited in the North Dakota State Fossil Collection, Johnsrud Paleontology Laboratory, North Dakota Heritage Center, Bismarck, North Dakota, with curatorial data as given in Table 1.

Diagnosis. A species of *Ischyodus* that differs from all other species in this genus by several mandibular tooth plate and palatine tooth plate characteristics. Mandibular tooth plate characteristic unique to this species is the unequally bifurcate median tritor in which the tip of the outer branch lies directly posterior to the anterior outer tritor and the inner branch extends beyond the anterior tip of the anterior outer tritor. The presence of an indistinct accessory median tritor is also unique to this species. Palatine tooth plate characteristics that differentiate this species from other *Ischyodus* species include the elongate median tritor that extends beyond the posterior inner tritor and the distinctly curved, elongate outer tritor.

Description

Mandibular tooth plate. Mandibular tooth plate is large, robust, and nearly complete except for the absence of a small portion of the basal margin between the median tritor and posterior outer tritor (Table 1; Pl. 1, figs 10–12; Text-fig. 3). Five tritors are present: symphyseal tritor, anterior inner tritor, median tritor, anterior outer tritor and posterior outer tritor. An indistinct accessory median tritor is present. View from the basal margin indicates that this accessory median tritor is internally connected to the median tritor. Median tritor is massive and unequally bifurcate. Tip of the outer branch of the median tritor is directly posterior to, and in line with, the anterior outer tritor. Tip of the inner branch of the median tritor ends equal with or extends slightly beyond the anterior tip of the anterior outer tritor. Axes of the posterior outer tritor, anterior outer tritor and median tritor are distinct, straight and subparallel to one another, whereas the axis of the anterior inner tritor forms an acute angle with these. Anterior inner tritor is on a raised, blade-like projection of the tooth plate.

Palatine tooth plate. Palatine tooth plate is triangular in shape from the occlusal view, laterally compressed and more gracile than the mandibular tooth plate (Table 1; Pl. 1, figures 1–9; Text-fig. 3). Four tritors are present: anterior inner tritor, posterior inner tritor, median tritor and outer tritor. These tritors vary in width but are always closely spaced and in the same relative position. The anterior inner tritor is elongate as seen clearly on the most complete palatine specimen (Pl. 1, figure 5; Text-fig. 3). The median tritor extends anterior of the posterior inner tritor. The outer tritor is elongate and distinctly curved.

Vomerine tooth plate. The morphology of the vomerine tooth plate of this species is unknown because no specimens of vomerine tooth plates have been found.

Discussion. It is appropriate to describe the means by which *Ischyodus rayhaasi* can be distinguished from those species to which it is closest either morphologically or chronologically. The following characteristics separate *I. rayhaasi* from *Ischyodus bifurcatus* Case, 1978. The mandibular tooth plate' of *I. rayhaasi* is proportionally more elongate than *I. bifurcatus*. It possesses an indistinct accessory median tritor; *I. bifurcatus* does not. The median tritor of *I. rayhaasi* is much less bifurcate than in *I. bifurcatus* and the bifurcation in *I. rayhaasi* is distinctly unequal. The tip of the outer branch of the median tritor almost touches, and is directly posterior of, the anterior outer tritor in *I. rayhaasi*, whereas in *I. bifurcatus* the outer branch does not extend to the anterior outer tritor and is displaced more toward the posterior outer tritor. In *I. rayhaasi*, the tip of the inner branch of the median tritor extends beyond the anterior outer tritor, whereas in *I. bifurcatus* the inner branch does not extend to the anterior outer tritor. The anterior inner tritor is distinct in *I. rayhaasi* but is 'dormant' in *I. bifurcatus* Case, 1978.

Palatine tooth plate characteristics also separate *I. rayhaasi* from *I. bifurcatus*. The palatine tooth plate tritors are more elongate in *I. rayhaasi* than in *I. bifurcatus*. The median tritor is much more elongate in *I. rayhaasi* than in *I. bifurcatus* and extends beyond the posterior inner tritor, which it does not do in *I. bifurcatus*. The outer tritor of *I. rayhaasi* is distinctly curved compared with the straight outer tritor of *I. bifurcatus*. The Campanian species, *I. bifurcatus*, ranges into deposits of Early Maastrichtian age and is evidently closely related to *I. rayhaasi* but is distinct from it morphologically and stratigraphically (Text-fig. 4).

Ischyodus rayhaasi differs from *Ischyodus dolloi* Leriche, 1902, in the following ways. The mandibular tooth plate of *I. rayhaasi* has a bifurcating median tritor where the inner branch of the median tritor extends beyond the anterior outer tritor. *I. dolloi* does not have a bifurcating median tritor. A distinct accessory median tritor is present on the mandibular tooth plate of *I. dolloi*. This accessory median tritor is less distinct in *I. rayhaasi*. The palatine tooth plate of *I. rayhaasi* possesses a more elongate anterior inner tritor than *I. dolloi*. The outer tritor is segmented and composed of several elements in *I. dolloi*, whereas the outer tritor of *I. rayhaasi* is distinct and undivided.

The median mandibular tritor of the long-ranging *Ischyodus thurmanni* Pictet and Campiche, 1858, is not bifurcate and is not as massive as in *I. rayhaasi*. An accessory median tritor is not present on the mandibular tooth plate of *I. thurmanni*. The outer tritor of the *I. rayhaasi* palatine tooth plate is much longer and is curved compared with the shorter and straight palatine outer tritor of *I. thurmanni*. Tritors of the mandibular tooth plate of *Ischyodus lonzeensis* Leriche, 1929, are elongate, narrow and small compared with the massive median mandibular tooth plate tritor of *I. rayhaasi*. Although the outer palatine tooth plate tritor of *I. lonzeensis* is elongate, it is not curved as it is in *I. rayhaasi*.

The chimaeroid specimen illustrated by Feldmann and Palubniak (1975, fig. 12) from the Fox Hills Formation of North Dakota is lost (R. M. Feldmann, pers. comm. 1998). The specimens figured by Waage (1968) from the Fox Hills Formation of South Dakota were not examined for this study. These illustrated specimens, identified by the respective authors as *Mylognathus priscus*, are fragmental mandibular tooth plates. We believe they are *Ischyodus rayhaasi* because of the unequally bifurcating median tritors with inner branches that extend nearly beyond the anterior outer tritors and outer branches that extend to the anterior outer tritors.

Popov and Ivanov (1996, p. 55) referred to chimaeroid fossils found in Maastrichtian rocks in the Volga region of Russia as *Ischyodus ?bifurcatus*. They described the medial mandibular tritor of *I. ?bifurcatus* as significantly stretched medially and stated that an accessory tritor is present on the mandible. They also noted that the accompanying palatine is morphologically weak compared with *Ischyodus bifurcatus*. Their descriptions and accompanying drawings of the mandibular and palatine tooth plates suggest to us that their *I. ?bifurcatus* is a synonym of *Ischyodus rayhaasi*.

Geographical distribution and stratigraphic range. Geographical distributions of Fox Hills marine organisms have been of interest since Erickson (1973, 1974) began analysis of faunal origins and the closing history of the WIS. *Ischyodus rayhaasi* is known from south-central North Dakota (Text-fig. 1; Table 1) and north-central

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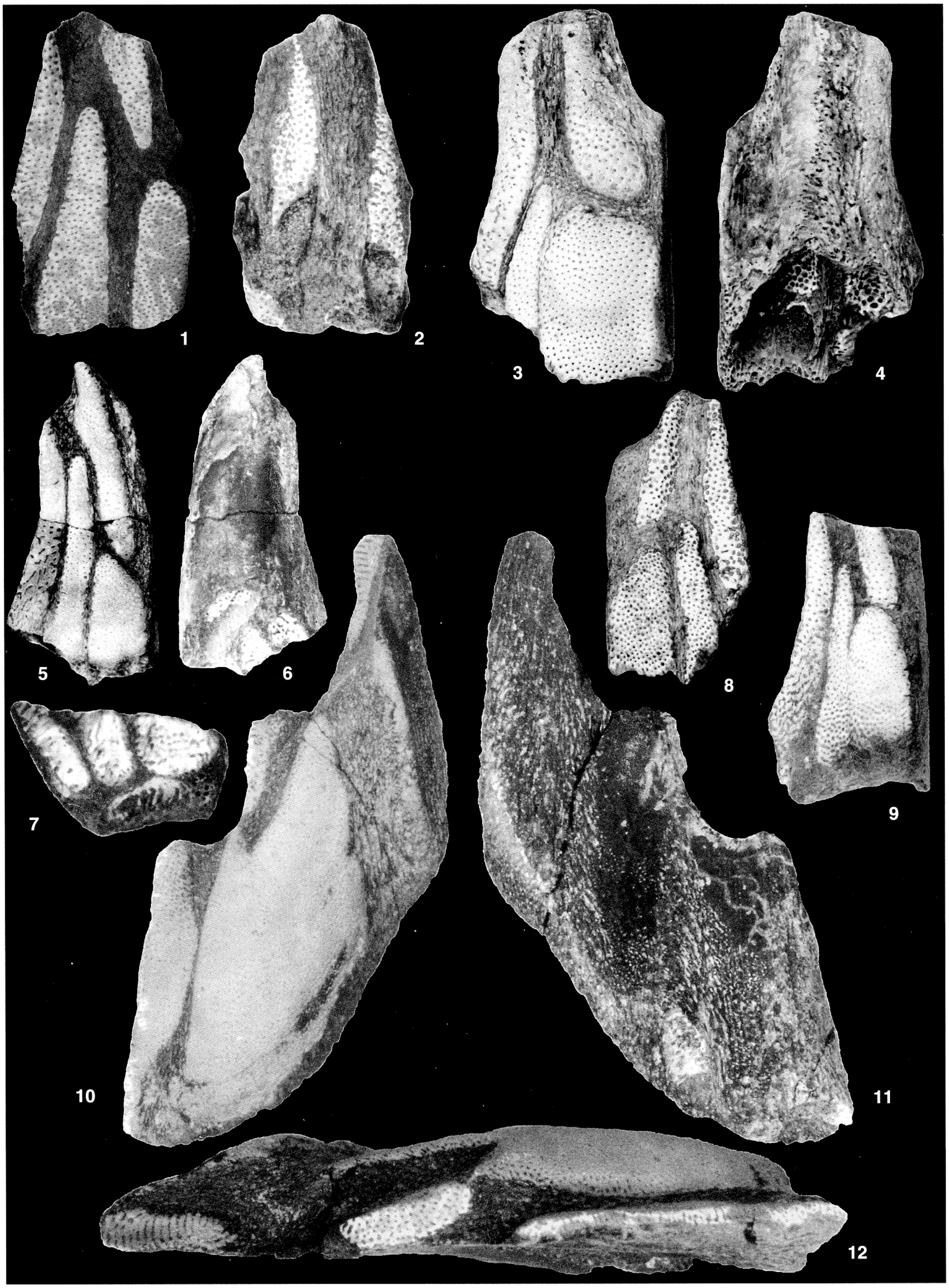
EXPLANATION OF PLATE 1

Figs 1–12. *Ischyodus rayhaasi* sp. nov. 1–2, right palatine tooth plate; paratype, ND 95-13.32, Logan County, North Dakota (NDSFC locality number LO1); Fox Hills Formation. 1, occlusal, and 2, abocclusal views; ×2. 3–4, right palatine tooth plate; paratype, ND 00-58.1, Morton County, North Dakota (NDSFC locality number MO34); Fox Hills Formation. 3, occlusal, and 4, abocclusal views; ×2. 5–7, right palatine tooth plate; paratype, ND 95-15.1, Morton County, North Dakota (NDSFC locality number MO20); Breien Member of the Hell Creek Formation. 5, occlusal, 6, abocclusal, and 7, basal views; 5–6, ×2; 7, ×3. 8, left palatine tooth plate; paratype, ND 99-12.1, Morton County, North Dakota (NDSFC locality number MO3); Breien Member of the Hell Creek Formation; occlusal view; ×2. 9, right palatine tooth plate; paratype, ND 93-1.1, Morton County, North Dakota (NDSFC locality number MO27); Hell Creek Formation; occlusal view; ×2. 10–12, left mandibular tooth plate; holotype, ND 99-6.1; Logan County, North Dakota (NDSFC locality number LO64); Fox Hills Formation; 10, occlusal, 11, abocclusal, and 12, occlusal margin views; ×1·5.

South Dakota. It occurs in the Late Maastrichtian Fox Hills Formation, Breien Member of the Hell Creek Formation and other unnamed units within the Hell Creek Formation (Text-fig. 2). As noted, this species has also been recovered from Maastrichtian deposits in the Volga region of Russia (Popov and Ivanov 1996), indicating

PLATE 1



HOGANSON and ERICKSON, *Ischyodus*

Late Cretaceous *Ischyodus* species Ranges (Stahl 1999; Duffin 2001; this paper)

	Obradovich (1993)			*Ischyodus*	*I. townsendi*	*I. latus*	*I. brevirostris*	*I. gubkini*	*I. planus*	*I. incisus*	*I. minor*	*I. lonzeensis*	*I. thurmanni*	*I. yanshini*	*I. bifurcatus*	*I. rayhaasi* sp. nov.	*I. dolloi*	*I. williamsae*	*I. zinsmeisteri*	*I. mortoni*
		Holocene		0																
			QUAT.	0																
		Pleistocene		0																
				0																
		Pliocene		0																
				X																X
		Miocene	TERTIARY	X																X
		Oligocene																		
				o																
		Eocene		X																
				X													X	X	X	
		Paleocene		X													X			
			65·4 Ma																	
66		Late Maastrichtian		X												X	?			
68				X									X		X					
70 Ma	71·3 Ma	Early Maastrichtian		X									X		X					
72		Late Campanian		X									X	X	X					
74				X									X	X	X					
76				X									X	X	X					
78				X									X	X	X					
80 Ma				X									X	X	X					
82		Early Campanian		X									X		X					
84	83·5 Ma	Santonian	LATE CRETACEOUS	X								X	X		X					
86				X									X							
88	86·3 Ma	Turonian		X						X			X							
90 Ma				X						X	X		X							
92				X						X	X		X							
94	93·3 Ma	Cenomanian		X						X	X		X							
96				X					X	X			X							
98				X					X	X			X							
100 Ma	98·5 Ma	Albian	M. Cret.	X		X	X	X	X	X										
			Lt. Jur.	X	X															
			M. Jur.	X																
			E. Jur.	0																

TEXT-FIG. 4. Chart showing temporal ranges of *Ischyodus* species. Ranges are those for *Ischyodus* species accepted by Stahl (1999).

faunal dispersion and continuity between western North America and the interior of eastern Europe.

Ischyodus rayhaasi is a member of a clade of *Ischyodus* species that began to radiate in the Jurassic (Text-fig. 4). Popov and Ivanov (1996) have demonstrated a sequence of morphological developments in species of *Ischyodus* that suggest rapid evolution of tritor shape and arrangement during the Late Cretaceous. Bifurcation of the median tritor of the mandibular tooth plate in Late Cretaceous species of *Ischyodus*, which is particularly pronounced in *Ischyodus rayhaasi*, is of major importance in defining species. *I. rayhaasi*, which disappears at the end of the Cretaceous, is the last *Ischyodus* species to exhibit this character. The median tritor of the mandibular tooth plate of the Paleocene *Ischyodus dolloi* is not bifurcate, nor is it so in any other Tertiary *Ischyodus* species.

It is noteworthy that in both North Dakota and the Volga region of Russia *Ischyodus rayhaasi* is preserved in shallow-water facies in numbers and size ranges that suggest resident populations rather than occasional visitors. The broadening shallow shelves of epicontinental seas resulting from lowered sea level produced rich molluscan shallow marine and estuarine communities (Rhodes *et al.* 1972; Erickson 1973, 1978), which were enticing to chimaeroids. Species such as *Ischyodus bifurcatus* and *I. rayhaasi* were members of a group of opportunistic chimaeroids that invaded shallow waters to exploit these areas of high benthic molluscan productivity.

None of the Maastrichtian species of *Ischyodus* is known to have survived into the Paleocene, at which time a second radiation of *Ischyodus* seems to have occurred. Stahl and Chatterjee (2002) have recently illustrated a chimaeroid specimen from the Early Maastrichtian Lopez de Bertodano Formation on Seymour Island, Antarctica, which they identified as *Ischyodus dolloi*. Previously *I. dolloi* had only been reported from early Cenozoic deposits:

the Paleocene of Belgium and France (Leriche 1902), the Eocene of England (Gurr 1963; Ward 1973), the Late Eocene La Meseta Formation of Seymour Island, Antarctica (Ward and Grande 1991), the Paleocene Cannonball Formation of North Dakota (Cvancara and Hoganson 1993) and the Paleocene/Eocene of Russia (Popov 1996). Stahl and Chatterjee (2002) noted that the occurrence of *I. dolloi* in the Lopez de Bertodano Formation extends the stratigraphic range of that species by about 12 myr from the Paleocene into the Early Maastrichtian and geographically into the distant Southern Hemisphere, which suggested to them that the origin of the species by was there. They also pointed out that the chronological range extension of *I. dolloi* into the Cretaceous indicated that *I. dolloi* is the only species of chimaeroid known to be found on both sides of the K/T boundary. Their identification of the specimen as *I. dolloi* and their subsequent interpretations are based upon a single, badly eroded specimen, the illustration of which does not seem to warrant identification at the species level. The questioned Maastrichtian occurrence of *I. dolloi* in Text-figure 4 signifies our strong uncertainty of that assignment.

CONCLUSIONS

Twelve specimens of a callorhynchid chimaeroid were collected from the Late Maastrichtian Fox Hills and Hell Creek formations at several localities in south-central North Dakota. Analysis of both well-preserved mandibular and palatine tooth plates indicates that these specimens represent a new species. We have named this species *Ischyodus rayhaasi* in honour of a long time observer of Fox Hills and Hell Creek fossils and contributor of fossils to several museums including one of the paratypes of this species to the North Dakota State Fossil Collection.

Unlike extant chimaeroids that inhabit deep, marine waters, *Ischyodus rayhaasi* resided in shallow marine and estuarine areas of the northern part of the WIS during the Late Maastrichtian. This species also apparently lived in shallow oceans in the Volga region of Russia, implying cosmopolitan tendencies, at least in the Northern Hemisphere. *Ischyodus rayhaasi* was a member of a long-lasting clade whose members probably invaded and exploited high molluscan productivity areas of shallowing, Maastrichtian epicontinental seas. The genus ranged from the Late Jurassic into the Pliocene. *I. rayhaasi* is the youngest known Cretaceous species of that genus and it did not survive the K/T boundary extinction event. This finding is consistent with other studies that suggest that chondrichthyan taxa in the WIS were affected by extinction at the end of the Cretaceous (Cvancara and Hoganson 1993; Hoganson *et al.* 1996, 1997; Hoganson 2000; Hoganson and Murphy 2002) as was their molluscan food supply.

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