Abstract—The Smoky Hill Chalk Member of the Niobrara Chalk is an Upper Cretaceous marine deposit found in Kansas and adjacent states in North America. The rock, which was formed under the Western Interior Sea, has a long history of yielding spectacular fossil marine vertebrates, including fishes. Here, we present an annotated taxonomic list of fossil fishes (= non-tetrapod vertebrates) described from the Smoky Hill Chalk based on published records. Our study shows that there are a total of 643 referable paleoichthyological specimens from the Smoky Hill Chalk documented in literature of which 133 belong to chondrichthyan and 510 to osteichthyan. These 643 specimens support the occurrence of a minimum of 70 species, comprising at least 16 chondrichthyans and 54 osteichthyans. Of these 70 species, 44 are represented by type specimens from the Smoky Hill Chalk. However, it must be noted that the fossil record of Niobrara fishes shows evidence of preservation, collecting, and research biases, and that the paleofauna is a time-averaged assemblage over five million years of chalk deposition. Our historical review suggests that, whereas the number of described fish species from the Smoky Hill Chalk has declined in the last 75 years, the amount of research on fish taxa has constantly increased for the last three decades. We recognize three major periods of Smoky Hill Chalk paleoichthyological research: 1) between 1870 and 1879 due mostly to E. D. Cope’s effort in describing the majority of osteichthyan taxa; 2) between the late 1890s and into the early 1900s due primarily to efforts of new workers such as O. P. Hay, F. B. Loomis, A. Stewart, and S. W. Williston; and 3) since the mid-1960s. The recent resurgence in the study of fish taxa of the Smoky Hill Chalk appears to reflect the renewed interest in systematic ichthyology, biostratigraphy, and paleoecology.

INTRODUCTION

The Niobrara Chalk is an Upper Cretaceous marine deposit occurring in Kansas and adjacent states in North America. The rock formed under the Western Interior Sea, an epicontinental sea that extended in a generally north-south direction in the middle of the continent. The formation consists of two calcareous stratigraphic members: the 20-m-thick Fort Hays Limestone Member gradationally overlain by the 180-m-thick Smoky Hill Chalk Member (Hattin et al., 1987; Hattin, 1982). The Fort Hays Limestone yields vertebrate fossils, but only 12 taxa with small sample sizes are known from the member to date (Shimada, 1996a; Shimada and Everhart, 2003; Everhart, 2005b). On the other hand, the Smoky Hill Chalk is regarded as a fossil Lagerstätte and famous for yielding diverse and often spectacular fossil marine vertebrates (Bottjer, 2002: Fig. 1). They include chondrichthyan, osteichthyan fishes, and various tetrapods, such as marine turtles, mosasaurs, pleisosaurs, pterosaurs, and birds (for overview, see Everhart, 2005c). In addition, there are some dinosaur remains from the Smoky Hill Chalk, which apparently represent post-mortem terrestrial materials washed out to sea (e.g., Carpenter et al., 1995; Everhart and Hamm, 2005; Everhart and Ewell, in press).

Fossil vertebrates from the Smoky Hill Chalk are documented in diverse scientific literature sporadically published since the mid-1800s (e.g., Cope, 1868). The taxonomic composition of the vertebrate fauna, or part of the fauna, has been reviewed from time to time (e.g., Williston, 1900a; Stewart, 1900; Hay, 1903; Hussakof, 1908; Lane, 1945; Russell, 1988, 1993; Carpenter, 1990, 2003; Stewart, 1990a; Everhart, 2005c). Russell (1988) presented the first systematic list of vertebrate taxa from the Smoky Hill Chalk based on published literature supplemented with unpublished data. His study showed that the vertebrate paleofauna includes about 110 taxa, of which about 60% are non-tetrapod vertebrates (= ‘fishes’) and 40% tetrapods. Recently, Carpenter (2003) examined the vertebrate biostratigraphy of the Smoky Hill Chalk, which was based on his previous work (Carpenter, 1990) and partially similar to Stewart’s (1990a) work. One of the major shortcomings of Carpenter (1990, 2003) and Stewart’s (1990a) work is the lack of literature references and specific specimens that were used to base their occurrence data.

Because Russell’s (1988) taxonomic list included taxa based on unpublished data, and because Carpenter (1990, 2003) and Stewart’s (1990a) lists are not reproducible due to the lack of referred literature and specimens to support their occurrence data, uncertainty exists as to the exact taxonomic composition of the vertebrate fauna in the Smoky Hill Chalk. Since Russell (1988), Stewart (1990a), and Carpenter’s (1990, 2003, which is essentially based on his 1990 data) work, a number of papers which describe vertebrates from the stratigraphic member were published (e.g., Everhart et al., 2003; Hamm and Shimada, 2002b; Shimada, 1997f; Stewart, 1996, 1999a). Also, some taxa represented in the Niobrara vertebrate fauna underwent taxonomic revisions in recent years. Therefore, we determined that a collective review of vertebrate fauna of the Smoky Hill Chalk would make a significant contribution to the paleontology of the Niobrara Chalk (e.g., a review of Niobrara vertebrates in South Dakota by Martin et al., 1988).

In this paper, we focus on fossil fishes from the Smoky Hill Chalk of Kansas (Figs. 1-4; Table 1). We here present an annotated taxonomic list of fossil fishes described from the stratigraphic member base strictly on published records. We believe that our work illuminates the history of Niobrara fish research and serves as a useful research tool to those who wish to study fish taxa from the formation. The list also offers a historical perspective of Niobrara fish research and an opportunity to evaluate the current state of our knowledge of the Cretaceous ichthyofauna.

METHODS

The occurrences of fossil vertebrates from the Niobrara Chalk have been described in various media. For the purposes of this study, we only considered published papers that include specific catalogue numbers of specimens housed in public institutions. Data based on pictorial guidebooks (e.g., Liggett, 2001; McKinzie, 2002), unpublished dissertations and theses (e.g., Shimada, 1994d; Fielitz, 1999), as well as magazines, news me-
Order Chimaeriformes Obruchev, 1953

Family Ptychodontidae Jaekel, 1898

Genus Edaphodon Buckland, 1838

**Edaphodon sp.**

**Referred material**–BMNH P10343, dorsal fin spine (Stahl, 1999, fig. 143).

### Additional remarks (at order level)–Ichthyopriapus hubbsi

Hibbard, 1942, initially placed in “chimaeroid,” is now considered to be *nomen dubium*. The type specimen (KUVP 1136) is bony and considered to be part of partial skeleton of *Protosphyraena gladius* (Cope, 1873) (KUVP 465), with which was discovered associated (Schultze et al., 1982, p. 4; Stahl, 1999, p. 154).

**Subclass Elasmobranchii**

**Order incertae sedis**

**Family Ptychodontidae Jaekel, 1898**

**Genus Ptychodus Agassiz, 1835**

**Ptychodus anonymus** Williston, 1900a

**Referred material**–AMNH FF 19553, 201 associated teeth, several vertebral centra, pieces of calcified cartilages, and oral denticles (part of this specimen, including a set of associated denticles, is curated in LACM as LACM 138527); FHSM VP-14854, teeth and oral denticles (Everhart et al., 2003; Everhart and Caggiano, 2004; Everhart, 2005c, p. 63).

**Notes**–The taxonomy of *Ptychodus anonymus* is problematic because the type materials of this taxon (Williston, 1900a, pl. 11, figs. 5–8, 16–18, 20–22, 24; Williston, 1900b, pl. 29, figs. 5–8, 16–18, 20–22, 24), that were collected from pre-Niobrara deposits (“Benton” formation), appear to include teeth that belong to *P. mammillaris* (Williston, 1900b, pl. 29, figs. 5, 6, 16, 18; see Herman, 1977, p. 59). Williston (1900a, p. 32; 1900b, p. 241) and Stewart (1990a) noted the occurrence of *P. anonymus* from the Smoky Hill Chalk of Kansas (specimens unspecified). Everhart (2005c, fig. 4.7) erroneously noted an associated tooth set of *P. anonymus* (FHSM VP-2223) as “*P. mortoni.*”

**Ptychodus cf. P. latissimus** Agassiz, 1843

**Referred material**–FHSM VP-14853, tooth (Everhart et al., 2003; Fig. 2A).

**Notes**–The exact taxonomic placement of the specimen (Fig. 2A) is uncertain within the genus *Ptychodus* because the total intraspecific morphological range of teeth in most *Ptychodus* species is poorly known. There is a possibility that the tooth may belong to one of the other *Ptychodus* species described from the Smoky Hill Chalk of Kansas.

**Ptychodus martini** Williston, 1900a

**Referred material**–FHSM VP-2121, tooth (Hamm, 2002; Hamm and Shimada, 2004); KUVP 55277, holotype, tooth set (for review, see Schultze et al., 1982, p. 13; Hamm and Shimada, 2004).

**Notes**–Hamm and Everhart (1999) reported the occurrence of 170 associated teeth of *Ptychodus martini*, but the specimen remains undescribed. Everhart et al. (2003) noted the occurrence of *P. martini* from...
the Smoky Hill Chalk of Kansas (specimens unspecified). Everhart (2005c, p. 65) erroneously reported the type specimen of *P. martini* (KUVP 55277) as “FHSM VP-55271.”

**Ptychodus mortoni** Mantell, 1839

**Referred material**—FHSM VP-15013, tooth (Everhart et al., 2003); KUVP 55269, tooth set; KUVP 55270, tooth set (for review, see Schultze et al., 1982, p. 14); KUVP 59041, partial skeleton (Stewart, 1980; Schwimmer et al., 1997, p. 77; Everhart and Caggiano, 2004, p. 129; Everhart, 2005c, p. 54).

**Notes**—Stewart (1980) used preserved calcified vertebrae in *Ptychodus mortoni* (KUVP 59041) to suggest that Ptychodontidae is a neoselachian shark (note: recent studies suggest that Ptychodontidae may be a hybodontiform (i.e., non-neoselachian) shark: Cuny et al., 2003, 2004, 2005).

**Ptychodus polygyrus** Agassiz, 1839

**Referred material**—FHSM VP-76, VP-2123, and VP-15008, isolated teeth (Caggiano and Everhart, 2003; Everhart et al., 2003; Everhart, 2005c, p. 65); KUVP 55237, tooth (Williston, 1900b, p. 240; catalogue number based on Schultze et al., 1982, p. 14).

**Additional remarks** *(at genus level)*—Russell (1988) cited Herman (1977, p. 59) for the occurrence of *Ptychodus mammillaris* Agassiz, 1839, from the Smoky Hill Chalk, which was based on teeth described by Williston (1900b, pl. 29, figs. 2, 3, 5, 6, 8, 16, 18). However, those *Ptychodus* teeth apparently occurred in pre-Niobrara deposits (“Benton” formation: Williston, 1900b, p. 241, 243), dismissing the occurrence of *P. mammillaris* from the Smoky Hill Chalk on this ground.

Russell (1988) listed *Ptychodus occidentalis* Leidy, 1868, in the Smoky Hill Chalk vertebrate fauna. However, *P. occidentalis* is a Cenomanian–Turonian taxon (see Welton and Farish, 1993, p. 64; Shimada et al., 2006), and the general area where Leidy’s (1868) original material was collected (“a few miles east of Fort Hays, Kansas,” p. 207) lacks exposures of the Smoky Hill Chalk, but those of the Greenhorn and Carlile formations (Cenomanian–Turonian). This fact eliminates the Niobrara record of *P. occidentalis*.

Hattin (1996) described a cirripede-bearing coprolite-like specimen (KUP 286929) interpreted to be a possible *Ptychodus* regurgitate. Kauffman (1972) suggested that breakage in inoceramid shells in the Niobrara Chalk is due to *Ptychodus* predation (see also Stewart, 1988). Bardack (1965b, p. 9) noted FHSM “10688-288” (uncertain catalogue number) and VP-1652 as “*Ptychodus* sp.” Everhart and Caggiano (2004, p. 129) listed the following specimens to consist of “associated *Ptychodus* tooth sets” (species unspecified): FHSM VP-2222, VP-2223, and VP-14854.

**Order Lamniformes** Berg, 1958

**Family Mitsukuriniidae** Jordan, 1898

**Genus Scapanorhynchus** Woodward, 1889

**Scapanorhynchus raphidon** (Agassiz, 1844)
Referred material—FHSM VP-13961, five associated teeth (Hamm and Shimada, 2002a, 2002b); KUVP 13522, one tooth (Williston, 1900a, 1900b; for review, see Schultz et al., 1982).

Notes—Williston’s (1900a, pl. 8, fig. 2, pl. 14, fig. 4; 1900b, pl. 26, fig. 2, pl. 32, fig. 4) Scapanorhynchus raphiodon tooth probably from the Niobrara Chalk of Kansas is considered to be a tooth of *Cretothyrella mantelli* (KUVP 13522: Schultz et al., 1982, p. 7).

Family Odontaspidae Müller and Henle, 1839

Genus *Johnlongia* Siverson, 1996

*Johnlongia* sp.

Referred material—FHSM VP-15545, tooth (Everhart et al., 2004; Shimada, Ewell et al., 2004).

Notes—Shimada, Ewell et al. (2004) noted that FHSM VP-15545 is morphologically unique and may represent a new taxon within the genus *Johnlongia*. They also noted that its occurrence represents the stratigraphically youngest *Johnlongia* specimen in the world.

Additional remarks (at family level)—Russell (1988, p. 25) listed “*Odontaspis* sp.” in his faunal list of the Smoky Hill Chalk based on his personal communication with J. D. Stewart. However, the presence of the genus *Odontaspis* from the stratigraphic unit cannot be confirmed because Russell (1988) did not refer to any specific specimen.

Family Cretothyrididae Glikman, 1958

Genus *Cretalamna* Glikman, 1958

*Cretalamna appendiculata* (Agassiz, 1843)

Referred material—FHSM VP-14851, tooth; FHSM VP-14852, tooth (Hamm et al., 2003); LACM 128126, partial skeleton including ca. 120 teeth (Shimada, 2005b; Fig. 2B).

Notes—Williston (1900a, p. 37; 1900b, p. 247) suggested that this species occurs from the Niobrara Chalk of Kansas but did not specify the specimens (and may be lost: see Schultz et al., 1982).

Additional remarks (at genus level)—The genus has been commonly referred to *Cretalamna*, but as pointed out by Siverson (1999), the original spelling of the genus by Glikman (1958) is *Cretalamna*, and that usage is followed here.

Genus *Cretothyrella* Glikman, 1958

*Cretothyrella mantelli* (Agassiz, 1843)

Referred material—CMN 40906, caudal and posterior precaudal vertebrae with hypochordal rays and placoid scales (Shimada, Cumbaa et al., 2004, Shimada et al., this volume); FFHM 1972.196, tooth (Everhart, 2005c, p. 50, 51; figs. 4.2, 4.3; Everhart, 2005c) and elasmosaurid plesiosaurs (Everhart, 2005a) as well as hadrosaurid and nodosaurid dinosaurs (Hamm and Everhart, 2001; Everhart and Hamm, 2005; Everhart and Ewell, in press). Shimada et al. (2002) and Shimada and Everhart (2004) described a Xiphactinus audax specimen from the Smoky Hill Chalk (ESU 1004: see below) that has an embedded tooth of *Cretothyrella mantelli* (unnumbered). Everhart (2005c, p. 49–52, fig. 4.1; 2005e) discussed mosasaur specimens from the Smoky Hill Chalk of Kansas (FHSM VP-13284 and VP-13742) with one or more embedded *C. mantelli* teeth (unnumbered).

Family Anacoracididae Casier, 1947

Genus *Pseudocorax* Priem, 1897

*Pseudocorax laevis* (Leriche, 1906)

Referred material—FHSM VP-13959, tooth; FHSM VP-13960, tooth (Hamm et al., 2003; Fig. 2C).

Notes—Applegate (1970, p. 395) noted that FHSM has some teeth of *Pseudocorax affinis* (Agassiz, 1843), but he did not specify the specimens. Shimada (1997c) reported 20 associated teeth of “cf. *Pseudocorax* sp.” (KUVP 55060: the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); FHSM VP-13747, tooth tip embedded in a series of vertebrae with partial ribs of a mosasaur (FHSM VP-13746: Everhart, 2000a); FHSM VP-14010, partial skeleton (Corrado et al., 2003; Everhart, 2005c, p. 59, 61); KUVP 213, teeth; KUVP 247, partial skeleton; KUVP 1094, tooth (the catalogue number refers to a series of mosasaur vertebrae in which the tooth is embedded within); KUVP 49490, pectoral fin; KUVP 13520, tooth set; KUVP 13523, isolated teeth; KUVP 13536, tooth; KUVP 13589, isolated teeth; KUVP 40337, isolated teeth; KUVP 55060, fragmentary skeleton; KUVP 57294, tooth; KUVP 66120, tooth; KUVP 68979, fragmentary skeleton; KUVP 68980, tooth; KUVP 69102, partial skeleton; KUVP 69707, isolated teeth; KUVP 84872, tooth; KUVP 86418, tooth; KUVP 112807, tooth (Shimada, 1993b, 1997c; 1997d; 1997e; 1997f; Everhart, 2000); KUVP 13522, and 64541–64549, isolated teeth (Williston, 1900a, 1900b; for review, see Schultz et al., 1982); ROM 44656, tooth set; UNSM 1216, tooth set with some vertebrae (Shimada, 1997c, 1997e).

Notes—Until Glikman (1958) established the genus *Cretothyrella*, this taxon was referred to *Oxyrhina* Agassiz, 1843 (e.g., Eastman, 1895; Williston, 1900a, p. 36; Sternberg, 1907b) or *Isurus* Rafinesque, 1810 (e.g., Williston, 1900b, p. 246; Lane, 1945). Although further studies are needed, Shimada’s (2005a) phylogenetic analysis suggested that *Cretothyrella* may be closely allied to Allopiidae Bonaparte, 1838, based on the anatomical data taken from Niobrara specimens (e.g., Shimada, 1997d).

Applegate (1970, p. 398) noted that FHSM houses an “*Isurus* [= *Cretothyrella*] *mantelli*” specimen that preserves scales associated with a skull. He reported it as “no. 199,” but Shimada (1997d, p. 647) was not able to locate such a specimen. Bardack (1965b, p. 9) noted FHSM VP-2081 and VP-2714 as “*Isurus* sp.” Shimada (1995, 1996b) discussed some skeletal specimens of *C. mantelli* from the Niobrara Chalk of Kansas but did not refer to any specific catalogue numbers. Shimada and Hubbell (2001) discussed small symmetrical teeth of *C. mantelli* from the Niobrara Chalk of Kansas described by Eastman (1895). Shimada (2002) emended the tooth type identification of *C. mantelli* proposed by Shimada (1997c), who reconstructed the *Cretothyrella* dentition based on articulated tooth sets from the Smoky Hill Chalk.

In the Niobrara fossil record, putative bite marks of *Cretothyrella mantelli* are found on bones surfaces of mosasaurs (Everhart, 2005c, p. 50, 51; figs. 4.2, 4.3; Everhart, 2005e) and elasmosaurid plesiosaurs (Everhart, 2005a) as well as hadrosaurid and nodosaurid dinosaurs (Hamm and Everhart, 2001; Everhart and Hamm, 2005; Everhart and Ewell, in press). Shimada et al. (2002) and Shimada and Everhart (2004) described a Xiphactinus audax specimen from the Smoky Hill Chalk (ESU 1047: see below) that has an embedded tooth of *Cretothyrella mantelli* (unnumbered). Everhart (2005c, p. 49–52, fig. 4.1; 2005e) discussed mosasaur specimens from the Smoky Hill Chalk of Kansas (FHSM VP-13284 and VP-13742) with one or more embedded *C. mantelli* teeth (unnumbered).

Family Anacoracididae Casier, 1947

Genus *Pseudocorax* Priem, 1897
Referred material—AMNH FF 1909, two teeth (holotype of Galeocero crassidens Cope, 1872; as “C. falcatus” in Hussakof, 1908, p. 29); FHSM VP-2213, partial jaws with teeth (Shimada, 1994b; Everhart, 2005c, p. 58, 61; Shimada and Cicimurri, 2005); FHSM VP-13219, tooth (Squalicorax cf. S. kaupi; Shimada, 1997c, p. 929); KUVP 55188, 26 teeth and some calcified cartilage pieces; KUVP 55190, vertebrae and teeth (Shimada and Cicimurri, 2005); KUVP 64501–64510, 64512–64514, 64521, 64522, 64524, 64526, 64530, 64533, 64537, and 64539, teeth (as “C. falcatus” in Williston, 1900a, 1900b; for review, see Schultz et al., 1982, p. 10, 11); LACM 128007, vertebrae and teeth (Shimada and Cicimurri, 2005); YPM 56409, two teeth (Everhart, 2005c, p. 55).

Notes—Galeocero crassidens Cope, 1872, described only from the Niobrara Chalk of Kansas, is a synonym of Squalicorax kaupi. Compagno (1988, p. 404; 1990, p. 373, 374) described a partial skeleton of Squalicorax (LACM 16056), which he referred to it as “S. falcatus” (possibly = S. pristodontus).” The specimen could be S. kaupi based on this description. Shimada and Cicimurri (2005) described a S. kaupi specimen consisting of 42 teeth, placoid scales, and some calcified cartilage pieces (KUVP 229) that could have come from the Niobrara Chalk of Kansas. Everhart (2005c, fig. 4.4) illustrated a tooth of S. kaupi (unnumbered specimen).

Squalicorax pristodontus (Glikman in Glikman and Shvazhaite, 1971)

Referred material—FHSM VP-15009, tooth; FHSM VP-15010, tooth (Hamm et al., 2003; Everhart, 2005c, p. 58; Shimada and Cicimurri, this volume).

Notes—Everhart (2005c) illustrated a tooth of Squalicorax pristodontus (unnumbered specimen: fig. 4.4) and erroneously reported FHSM VP-15011 (tooth of S. kaupi: see Shimada and Cicimurri, this volume) as a tooth of S. pristodontus (p. 58).

Squalicorax volgensis (Glikman in Glikman and Shvazhaite, 1971)

Referred material—FHSM VP-644, tooth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the tooth: Beesson and Shimada, 2004, Fig. 2F).

Additional remarks (at genus level)—Until Whitley (1939) established the genus Squalicorax, the taxon was commonly referred to Corax Agassiz, 1843. Everhart (2004a, 2005c, p. 53) discussed mosasaur specimens (FHSM VP-3 and VP-13746) from the Smoky Hill Chalk of Kansas with putative Squalicorax bite marks.

Order Rajiformes Berg, 1940

Family Rhinobatidae Müller and Henle, 1838

Genus Rhinobatos Linck, 1790

Rhinobatos sp.

Refereed material—FHSM VP-644, “at least 70 teeth” (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beesson and Shimada, 2004; Fig. 2E).

Notes—Stewart (1990a, p. 24) and Everhart (2005c, table 13.1; 2005d) noted the occurrence of Rhinobatos sp. and Rhinobatos incertus, respectively, from the Smoky Hill Chalk (specimens unspecified).


Class Osteichthyes

Subclass Actinopterygii

Superorder Neopterygii

Order Pycnodontiformes Berg, 1940

Family Pycnodontidae Owen, 1846

Genus Micropycnodon Hibbard and Graffham, 1945

Micropycnodon kansensis (Hibbard and Graffham, 1941)

Referred material—KUVP 1019 (holotype), partial skull; KUVP 7030, partial skeleton (Dunkle and Hibbard, 1946; Everhart, 2005c, p. 98).

Notes—Hibbard and Graffham (1941) initially described the genus as Pycnomicrodon, which was later modified to Micropycnodon because the former name was preoccupied (Hibbard and Graffham, 1945). The two referred specimens were originally reported as from the Fort Hays Limestone, but they are now thought to have come from the Smoky Hill Chalk (Schultze et al., 1982, p. 22; but see also Stewart, 1990a, p. 21).

Genus Hadrodus Leidy, 1873

Hadrodus marshi Gregory, 1950

Referred material—YPM 1950 (holotype), partial skull (Gregory, 1950).

Family Nursallidae Blot, 1987

Genus Palaeobalistum Blainville, 1818

Palaeobalistum sp.

Referred material—FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beesson and Shimada, 2004; Fig. 2F).

Additional remarks (at order level)—Stewart (1990a, p. 24) noted the occurrence of “an undetermined pycnodont that is not Micropycnodon and is probably not Hadrodus” (specimens unspecified).

Order Semionotoformes Arambourg and Bertin, 1958

Family Lepisosteidae Cuvier, 1825

Genus Lepisosteus Lacépède 1803

Lepisosteus sp.

Referred material—KUVP 36243, fragmentary skeleton and scales (Wiley and Stewart, 1977; Everhart, 2005c, p. 99).

Order Pachycormiformes Berg, 1940

Family Pachycormidae Woodward, 1895

Genus Protosphyraena Leidy, 1857

Protosphyraena gladius (Cope, 1873)

Referred material—AMNH FF 1849 (holotype), pectoral fin; AMNH FF 2064, pectoral fin (Hay, 1903, p. 24, 25; Hussakof, 1908, p. 93); KUVP 439, 465, 49505, 60620, 66692, and 84867, specimens that
include or consist of pectoral fin (Stewart, 1988); KUVP 60692, pectoral fin and additional skeletal elements (Schwimmer et al., 1997, p. 77); LACM 126520, pectoral fin (Stewart, 1988).

**Protosphyraena nitida** (Cope, 1872)

**Referred material**—AMNH FF 1634, partial skull (Hay, 1903); AMNH FF 1893, partial skull (listed as the holotype by Hussakof, 1908, p. 93; cf. AMNH FF 2121); AMNH FF 1894, partial pectoral fin; AMNH FF 2105 (holotype of *Erisichthie penetrans* Cope, 1877c), rostrum (Stewart, 1988); AMNH FF 2121 (holotype), partial skull and pectoral fin (Hay, 1903; Everhart, 2005c, p. 89); FHSM VP-3251, pectoral fin (Stewart, 1988); KUVP 374, 417, 505, 12490, 49515, 55588, 55589, 60603, 60615, and 64495, specimens that include or consist of pectoral fin of *Protosphyraena nitida* (Stewart, 1988); KUVP 49514, pectoral fin; KUVP 125302, pectoral girdle and fin; LACM 129752, complete skull and fins (Everhart, 2005c, p. 92, fig. 5.6); LACM 133270, pectoral fin (Schwimmer et al., 1997, p. 77); NJSM 15021, partial skull; NJSM 15839, partial skull (Everhart, 2005c, p. 92).

**Notes**—*Erisichthie nitida* Cope, 1872, *E. penetrans* Cope, 1877c, *Pelecoperthus chirurgus* Cope, 1875, *Protosphyraena chirurgus* Cope, 1877c, Newton (1878) and Felix’s (1890) *P. penetrans*, and *P. obliquidens* Loomis, 1900, are all interpreted to be junior synonyms of *P. nitida* (e.g., see Hay, 1903).

**Protosphyraena perniciosa** (Cope, 1874)

**Referred material**—AMNH FF 1609 (paratype of *Pelecoperthus chirurgus* Cope, 1875), partial pectoral girdle (described as *Protosphyraena nitida* by Hussakof, 1908, p. 94); AMNH FF 1620, pectoral fin (Hay, 1903, p. 9–16; Stewart, 1988; listed as *P. tenuis* (Loomis, 1900) by Hussakof, 1908, p. 94); AMNH FF 1850 (holotype), pectoral fin spine; AMNH FF 1895, fragmentary pectoral fin; AMNH FF 1901, pectoral girdle and fin; AMNH FF 2058, pectoral fin (Stewart, 1898); FHSM VP-80, VP-4510, and VP-7623, specimens that include or consist of pectoral fin (Stewart, 1988); FHSM VP-10266, pectoral fin; FHSM VP-12059, pectoral fin base (Schwimmer et al., 1997, p. 77, 78); KUVP 356, 363, 366, 369, 372, 424–426, 431, 432, 440, 15388, 13706, 40294–40296, 49422, 49511, 49512, 49550, 49551, 55493, 55590, 55591, 56601–56603, 56611, 60604, 64496, and 64497, specimens that include or consist of pectoral fin (Stewart, 1988); KUVP 49530, hypural plate; KUVP 55500, caudal fin (McClung, 1908); KUVP 56614, pectoral girdles and fin (McClung, 1908; for review, see Schultz et al., 1982); KUVP 67877, caudal skeleton (Arratia and Lambers, 1996, p. 192); LACM 126004 and 126005, specimens that include or consist of pectoral fin; USNM 2-9-9-37, pectoral fin (Stewart, 1988).

**Notes**—AMNH FF 1609, now identified as *P. perniciosa*, was initially referred to as *Pelecoperthus chirurgus* by Cope (1875), a synonym of *Protosphyraena nitida*. Hay (1903, p. 8) pointed out that the specimen is not *Pelecoperthus chirurgus*. Stewart (1988) misspelled *Protosphyraena perniciosa* as "P. Hinciosa" (Everhart, 2005c, p. 91, 92). Everhart (2005c, fig. 5.5) illustrated a pectoral fin of *P. perniciosa* (unnumbered specimen).

**Protosphyraena tenuis** (Loomis, 1900)

**Referred material**—AMNH FF 205 and 211, specimens that include or consist of pectoral fin (Stewart, 1988); AMNH FF 2061, fragmentary pectoral fin (Hussakof, 1908, p. 94); KUVP 380, 384, 385, and 13587, pectoral fin (Stewart, 1900; for review, see Schultz et al., 1982, p. 24, 25); KUVP 426, 427, 429, 430, 49529, 49549, 55586, 55587, 55617, 60616, 70216, and 84807, specimens that include or consist of pectoral fin (Stewart, 1988); KUVP 433, pectoral fin; KUVP 125303, pectoral girdle and fin (Schwimmer et al., 1997, p. 77); KUVP 49491, posterior part of skeleton including caudal fin of “*P. c. P. tenuis*”; KUVP 119500, hypural plate (Arratia and Lambers, 1996, p. 192); LACM 135837, pectoral fin (Schwimmer et al., 1997, p. 77).

**Notes**—Stewart’s (1900) specimens of *Protosphyraena penetrans* (Cope, 1877c) are interpreted to belong to *P. tenuis* (see Schultz et al., 1982).

**Additional remarks** (at genus level)—Species of *Protosphyraena* were initially referred to the genus *Erisichthie* Cope, 1873 (see also Cope, 1877c). The taxonomic validity of the following three *Protosphyraena* species from the Niobrara Chalk of Kansas is uncertain: *P. dimidiata* (Cope, 1878) (AMNH FF 1635, holotype consisting of partial skull and vertebrae: Hay, 1903, p. 16–20; Hussakof, 1908, p. 92); *P. recurvirostris* Stewart, 1898d (see also Stewart, 1900; KUVP 373, holotype consisting of rostrum: Schultz et al., 1982, p. 24); and *P. segus* Hay, 1903 (based on Felix’s (1890) specimen of *P. nitida* skull: Hay, 1903, p. 20–22). These species are based on fin-less specimens, where the taxonomic identification of *Protosphyraena* species generally requires the knowledge about the morphology of pectoral fins (e.g., Stewart, 1988). In addition, no referred material can be relocated for *P. occidentalis* Stewart, 1900, from the Smoky Hill Chalk of western Kansas, and it is presently treated as *Protosphyraena* sp. (see Schultze et al., 1982, p. 24).

Crook (1892, fig. 1.9) illustrated a *Protosphyraena* specimen (catalogue number unspecified). Stewart (1898a, p. 28) described a new, unnamed species of *Protosphyraena* on the basis of a premaxillary specimen. He thought it might be a synonym of either *P. penetrans* (Cope, 1877c) or “*P. xiphoides*” (a probable misspelling of *P. ziphoides* Cope, 1877c), a species originally described as an *Erisichthie* taxon but now considered as a *Martinichthys* taxon: see below. Sternekorn (1913) described an unnamed species of *Protosphyraena* based on a complete set of pectoral fins. Hussakof (1908, p. 95) listed AMNH FF 1646 (fragmentary pectoral fin) as “*Protosphyraena* sp.” McClung (1908, pl. 13) reported the only known caudal fin of *Protosphyraena* (KUVP 55500: Everhart, 2005c, p. 93) in the Niobrara fossil record. Bardack (1965b, p. 9) noted FHSM VP-1659, VP-1660, VP-2024, and VP-2025 as “*Protosphyraena* sp.” Everhart (2005c) noted that at least 14 specimens of *Protosphyraena* are housed in YPM (e.g., YPM 42137, 42138, 42152, 42200, and 42285: p. 89), and he illustrated four *Protosphyraena* teeth (unnumbered specimens: fig. 5.4).
Division Teleostei

Order Ichthyodectiformes Bardack and Sprinkle, 1969

Family Ichthyodectidae Crook, 1892

Genus *Gillicus* Hay, 1898b

*Gillicus arcuatus* (Cope, 1875)

Referred material—AMNH FF 2326 (neotype), cranial elements (Bardack, 1965a); AMNH FF 7377, partial skull and scales (Hussakof, 1908, p. 74); AMNH FF 8582, 8586–8589, and 8603, cranial elements (Bardack, 1965a); AMNH FF 8563, mandible (Nelson, 1973, fig. 6A); CMNH 10118, neurocranium (Bardack, 1965a); FHSM VP-334 (referred to “FH 5026” by Bardack, 1965a, and “SMM 5026” by Bardack, 1976), nearly complete specimen inside abdominal cavity of *Xiphactinus audax* (FHSM VP-333) (Shimada and Everhart, 2004; Everhart, 2005c, p. 72, fig. 5.1); KUVP 3, 80, 127, 129, 133–135, 138, 143, 146, 339, 478, 738, 965, 10321, 11667, and 11669, cranial elements and/or pectoral girdle; USNM 21081, cranial elements (Bardack, 1965a).

Notes—Portheus arcuatus Cope, 1875, is a junior synonym of *Gillicus arcuatus*. The holotype could not be located, so Bardack (1965a) selected AMNH FF 2326 as a neotype. McClungh (1908) described the occurrence of *G. arcuatus* from the Niobrara Chalk of Kansas (specimens unspecified).

Genus *Ichthyodectodes* Cope, 1870

*Ichthyodectodes ctenodon* Cope, 1870

Referred material—AMNH FF 1611, partial skull (described as “Ichthyodectodes anaides Cope, 1872” in Hussakof, 1908, p. 76); AMNH FF 1622, neurocranium (Bardack, 1965a); AMNH FF 1628, vertebrae (described as “I. anaides” in Hussakof, 1908, p. 76); AMNH FF 1633, mandible (Nelson, 1973, fig. 6A); AMNH FF 1673, 1706, 1747, 2373, 7382, 8112, 8115, 8261, 8272, and 8590, cranial elements and/or vertebrae; AMNH FF 1719, cranial elements and pectoral girdle; AMNH FF 2332, fin ray fragments; AMNH FF 8443, nearly complete skeleton (Bardack, 1965a, Nelson, 1973, fig. 3C); AMNH FF 1903 (holotype of *P. lestrio Cope, 1873), partial skull and vertebrae (Hussakof, 1908, p. 88); AMNH FF 7296, pelvic girdle and fins; AMNH FF 7318, skull (described as *P. molossus* in Hussakof, 1908, p. 88); AMNH FF 7350, premaxilla and maxilla (Schwimmer et al., 1997; described as *P. thaumas* in Hussakof, 1908, p. 90); AMNH FF 322199, nearly complete skeleton (Osborn, 1904; see Everhart, 2005c, p. 76); BMNH P.11125, composite skeleton (Woodward, 1913); CM 1189, neurocranium and vertebrae; CM 4101 and 4102, composite of two individuals; CMN 8151, composite skeleton; CMN 8152 and 8152A, anterior portion of fish; CMNH 10421, various skeletal parts; DMNH 1667, nearly complete skeleton (Bardack, 1965a; Everhart, 2005c, p. 72, 73); ESU 1047, nearly complete skull and vertebrae (Shimada et al., 2002; Shimada and Everhart, 2004); FHSM VP-333 (Fig. 1; referred to “FH 5026” by Bardack, 1965a), nearly complete specimen containing *Gillicus arcuatus* (FHSM VP-334) inside its abdominal cavity (Schwimmer et al., 1997, fig. 1A; Shimada and Everhart, 2004; Everhart, 2005c, p. 72, fig. 5.1); FHSM VP-8935, cranial elements; FMN UF973, nearly complete skeleton (Bardack, 1965a, 1965b, p. 9); KUVP 1, 2, 3, 4, 88, 127, 135, 179, 275, 279, 287, 314, and 353, jaw elements (Stewart, 1899b); KUVP 103, composite skeleton; KUVP 124, 158, 160, 165, 166, 183, 262, 300, 477, 565, 735, 789, 930, 991, 9820, 9888, 11661, 11834, and 12011, cranial elements, vertebrae, and/or pectoral girdle (Stewart, 1900; Bardack, 1965a; Everhart, 2005c, p. 81); KUVP 155, cranial elements (holotype of *Xiphactinus brachygnathus* Stewart, 1899c); KUVP 245, partial skeletal elements as gastric residues of *Cretorychirina mantelli* (KUVP 247: Shimada, 1997a); NAMAL 2000-0925-099, complete skeleton (Shimada and Everhart, 2004; Everhart, 2005c, p. 73); SDNMH 63.01 and 63.02, nearly complete skeleton; SDSMS 2510 (now at Science Museum of Minnesota, St. Paul), partial skeleton; USNM 52 (holotype), partial first pectoral fin ray; USNM 1495, nearly complete skeleton; USNM 1646, 3782, 4207, 11554, and 11653, cranial elements; USNM 11178, vertebra; USNM 11650 and 21375, nearly complete skeleton (Bardack, 1965a; Everhart, 2005c, p. 76, fig. 2.2); YPM 2177, nearly complete skeleton (Thorpe, 1934).

Notes—Synonyms of *Xiphactinus audax* are: *Saurocephalus audax* Cope, 1870, *S. thamus Cope, 1870, Portheus molossus Cope, 1871 (“P. molossus,” a probable misspelling, in Sternberg, 1905, p. 127; “P. colos,” a probable misspelling, in Sternberg, 1907b, p. 122); *P. thamus Cope, 1872, P. lestrio Cope, 1873, P. mudgei Cope, 1874, P. lowii Cope, 1876, X. brachygnathus Stewart, 1899c. Hussakof (1908, p. 90) listed the following specimens as “Portheus sp.”: AMNH FF 1683 (fragmentary pectoral fin rays), 1688 (scapula and partial pectoral fin), 3742 (fragmentary mandible), 3760 (pectoral girdles), and 3788 (three neural arches). Bardack (1965a, table 3) reported another composite specimen of this species housed in Oakley, Kansas Public School numbered 13-25. Other papers that describe the occurrence of this taxon from the Niobrara Chalk of Kansas include papers by Crook (1892), Hay (1898a, 1898b, 1899a, 1899b, 1899c, 1900), Cope (1870), Osborn (1904), Sternberg (1905, 1907a, 1907b), and McClungh (1908). Beamon (2001) discussed a *X. audax* specimen in FHSM without referring to a specific catalogue number, but his description suggests that it is FHSM VP-333 (Fig. 1). Everhart (2004b) reported some vertebra of *X.*
andax (unnumbered) associated with a plesiosaur remain (USNM 9468) from the Smoky Hill Chalk of Kansas.

Family Saurodontidae Cope, 1871
Genus Prosaurodon Stewart, 1999a
Prosaurodon pygmaeus (Loomis, 1900)

Referred material– BSPHG 1893x43, mandible; FMNH PF3337, partial skeleton; KUVP 56637, mandible; KUVP 56638, mandibles; KUVP 56639, mandible; LACM 128316, jaw elements; LACM 141422, partial skull (Stewart, 1999a).

Genus Saurocephalus Harlan, 1824
Saurocephalus lanciformis Harlan, 1824

Referred material– AMNH FF 2073, fragmentary maxilla (Hussakof, 1908, p. 97); AMNH FF 7355 (holotype of Saurocephalus pamphagus Hay, 1899), skull parts; AMNH FF 7373, jaw parts; FMNH PF902, neurocranium and jaws; KUVP 109, mandibles; KUVP 154, upper jaw and predentary (Bardack and Sprinkle, 1969).

Notes– Synonyms of Saurocephalus lanciformis are: S. arapahovius Cope, 1872, S. dentatus Stewart, 1898a, and S. pamphagus Hay, 1899. The species was also discussed by Loomis (1900).

Genus Saurodont Hays, 1830
Saurodont leonis Hays, 1830

Referred material– AMNH FF 1614, mandible (Hussakof, 1908, p. 98; Nelson, 1973, fig. 3A); AMNH FF 1648, skull (Bardack and Sprinkle, 1969); AMNH FF 1906 (holotype of Saurocephalus goodeanus (Cope, 1877b)), partial skull, AMNH FF 7354, neurocranium and jaws; AMNH FF 8323, pectoral girdle; AMNH FF 8544, partial skull and vertebrae; FHSM VP-11322, skull and vertebral column; FMNH PF1333, skull; FMNH PF3337, skull, vertebræ, and fins; FMNH PF3741, complete fish; KUVP 142, mandibles and quadrate; KUVP 153, maxilla and predentary; KUVP 155, maxilla and dentary; KUVP 161, skull (holotype of Saurodon xiphirostris Stewart, 1898c); KUVP 212 (holotype of Daptinus broadheadi Stewart, 1898a); KUVP 343, skull; KUVP 28713, mandibles and right maxilla (Bardack and Sprinkle, 1969); KUVP 180, skull (Everhart, 2005c, fig. 5.2); MCZ 5342, jaws; YPM 3942, neurocranium (Bardack and Sprinkle, 1969).

Notes– Synonyms of Saurodon leonis are: Saurocephalus phlebotomus Cope, 1870, Ichthyodectes goodeanus (Cope, 1877b), S. goodeanus (Cope, 1877b), Daptinus broadheadi Stewart, 1898a (genus Daptinus was erected by Cope, 1873), Saurodon xiphirostris Stewart, 1898c, S. broadheadi (Stewart, 1898a) (e.g., see Loomis, 1900), S. jeron Stewart, 1898c. Bardack (1965b, p. 9) noted FHSM VP-1650 as “Saurodon sp.”

Additional remarks (at family level)–Hussakof (1908, p. 98) referred the following three specimens to “Saurocephalid indet.:” AMNH FF 1606, partial skull; AMNH FF 1607, partial skull; AMNH FF 1911, vertebrae.

Order Tseltaliformes Nelson, 1994
Family Plethodidae Loomis, 1900
Genus Bananogmius Whiteley, 1940
Bananogmius aratus (Cope, 1877a)

Referred material– AMNH FF 2403 (holotype), nearly complete skeleton (Hay, 1903, p. 34–41; Hussakof, 1908, p. 61, fig. 30; Nelson, 1973, fig. 8B; Taverne, 2000a, 2000d, 2001c).

Bananogmius favirostris (Cope, 1877b)

Referred material– AMNH FF 2109 (paratype), partial skull; AMNH FF 2111 (holotype), partial skull and vertebrae (Hay, 1903, p. 30–34; Hussakof, 1908, p. 62; Nelson, 1973, fig. 6D; Taverne, 2001c).

Additional remarks (at genus level)– Species of Bananogmius have been referred to the genera Beryx Stewart, 1898d, Anogmius Cope, 1877a (spelled Agnomius by Loomis, 1900), Osmorhizodus Agassiz, 1843, and Ananogmius White and Moy-Thomas, 1940 (for review, see Schulze et al., 1982; Taverne, 2001c). Nelson (1973, figs. 6C, 7) illustrated AMNH FF 3072, a partial skeleton of “Bananogmius sp.”

Genus Luxilistes Jordan, 1924
Luxilistes striolatus Jordan, 1924

Referred material– KUVP 295 (holotype), skull and trunk (Taverne, 2002a; Everhart, 2005c, p. 97).

Notes–The holotype is the only known specimen of this taxon.

Genus Syntegmodus Loomis, 1900
Syntegmodus altus Loomis, 1900

Referred material– AMNH FF 2112 (neotype), partial skull (Taverne, 2001b; Everhart, 2005c, p. 96).

Notes– Whereas Hussakof (1908, p. 61) identified AMNH FF 2112 as “Anogmius altus?,” Hay (1903, p. 41–46) placed Syntegmodus in Anogmius Cope, 1877a, a junior homonym replaced by Bananogmius Whiteley, 1940. Recently, Taverne (2001b) suggested that Syntegmodus is a distinct genus and is not a synonym of Bananogmius. The holotype was destroyed during the Second World War in Germany, and the neotype is the only known specimen of this taxon.

Genus Niobrara Jordan, 1924
Niobrara encarsia Jordan, 1924

Referred material– KUVP 179 (holotype), complete skeleton (Taverne, 2001a; Everhart, 2005c, p. 97).

Notes– The holotype is the only known specimen of this taxon.

Genus Martinichthys McClung, 1926
Martinichthys brevis McClung, 1926

Referred material– FHSMP VP-15567, rostrum (Everhart, 2005c, fig. 5.7); KUVP 497 (holotype), nearly complete skull; KUVP 40015, partial skull (Taverne, 2000b; Everhart, 2005c, p. 93).

Martinichthys ziphioides (Cope, 1877c)

Referred material– AMNH FF 2131 (holotype), rostrum (Hay, 1903, p. 22–24; Hussakof, 1908, p. 95); KUVP 498, partial skull; KUVP 499 (holotype of Martinichthys latus McClung, 1926), 500 (holotype of M. alternatus McClung, 1926), 501 (holotype of M. intermedius McClung, 1926), 502 (holotype of M. acutus McClung, 1926), 503 (paratype of M. acutus McClung, 1926), 504 (holotype of M. gracilis McClung, 1926), 506, and 507, rostral specimens (Taverne, 2000b; Everhart, 2005c, p. 93).

Notes– This species was initially assigned to the genus Erisichthe Cope, 1873, by Cope (1877c), and it was subsequently assigned to the genus Protosphyraena Leidy, 1857 (e.g., Loomis, 1900; Hay, 1903) until McClung (1926) established the genus Martinichthys. Taverne (2000b) synonymized the following species with Martinichthys ziphioides (Cope, 1877c): M. acutus McClung, 1926, M. alternatus McClung, 1926, M. gracilis McClung, 1926, M. intermedius McClung, 1926, and M. latus McClung, 1926.

Additional remarks (at genus level)– Everhart and Everhart (1993) noted that the occurrences of Martinichthys specimens are restricted to the lower one third of the Smoky Hill Chalk. Everhart and Everhart (1994) reported a rostral specimen of Martinichthys from the Smoky Hill Chalk (unnumbered specimen; species unspecified) that shows bite marks of an undetermined vertebrae. Besides FHSMP VP-15567 (rostrum of M. brevis; see above), Everhart (2005c, p. 95, 96) noted additional 18 Martinichthys specimens in FHSMP (VP-15549 – VP-15566, and VP-15568) of which one of them (VP-15568) may belong to an undescribed taxon.
Genus *Pseudothryptodus* Loomis, 1900

*Pseudothryptodus intermedius* Loomis, 1900

Referred material—None (see “Notes” below).

Notes—The only specimen of this taxon, the holotype, was destroyed during the Second World War in Germany (Taverne, 2003).

Genus *Thryptodus* Loomis, 1900

*Thryptodus zitieli* Loomis, 1900

Referred material—AMNH FF 19557, rostrum; KUVP 456, 457, and 459, rostral specimens (Taverne, 2000c); KUVP 25899, rostrum (Taverne, 2003; Everhart, 2005c, p. 96).

Notes—The holotype was destroyed during the Second World War in Germany (Shimada and Schumacher, 2003; Everhart, 2005c, p. 96, fig. 5.8). Stewart (1900, p. 391, 392) and Hay (1903, p. 40, 41) suggested that *Thryptodus* is a synonym of *Anogmius* Cope, 1877a, a junior homonym replaced by *Bananogmius* Whitley, 1940. Recently, Taverne (2001c) suggested that *Thryptodus* is a distinct genus and is not synonymous with *Bananogmius*. Everhart (2005c, p. 97) noted the destruction of a *Thryptodus* specimen (FHSM VP-15571) that consists of “most of the skull and several vertebrae.”

Genus *Plethododus* Dixon, 1850

*Plethododus rotundus* (Loomis, 1900)

Referred material—None (see “Notes” below).

Notes—The holotype (partial skull) described under the name *Thryptodus rotundus* by (Loomis, 1900) is the only known specimen of this taxon, and it was destroyed during the Second World War in Germany. Taverne (2000c) placed this species in the genus *Plethododus*; however, the taxonomic status of the genus *Plethododus* remains unresolved (see Cavin and Forey, 2001).

Genus *Pseudanogmius* Taverne, 2002b

*Pseudanogmius maiseyi* Taverne, 2002b

Referred material—AMNH FF 1116 (paratype), partial skeleton (as “AMNH 1616” in Hay, 1903, fig.15, and in Hussakof, 1908, p. 62); AMNH FF 1977 (paratype), caudal skeleton; AMNH FF 8129 (holotype), partial skeleton (Taverne, 2002b; Everhart, 2005c, p. 97).

Notes—The taxon was referred to “*Anogmius* sp.” by Hay (1903) and Hussakof (1908), and “*Bananogmius* sp.” by Nelson (1973, fig. 8C).

Genus *Pentanogmius* Taverne, 2000c

*Pentanogmius evolutus* (Cope, 1877b)

Referred material—AMNH FF 2101 (holotype), jaw fragment (Hussakof, 1908, p. 62; Hay, 1903, p. 46, 47; Nelson, 1973, figs. 2D, 5B; AMNH FF 2137, cranial elements and scapula; AMNH FF 3073, cranial elements; AMNH FF 3074, cranial elements and vertebrae; AMNH FF 7358, cranial elements; AMNH FF 8319, complete caudal fin (Nelson, 1973, figs. 5C, 5D, 6B; Taverne, 2004); BMNH P.10159, partial skeleton (Taverne, 2000a); KUVP 2, complete skeleton; KUVP 6, ceratohyal; KUVP 11, glossohyal and paraphrenoid; KUVP 14, mandibles and ceratohyal; KUVP 16 (cf. Taverne, 2000a, 2000d), tail; KUVP 273, tail; KUVP 308, partial skull; KUVP 12083, partial skull and vertebrae (for review, see Schultz et al., 1982); KUVP 4, partial skull (as “*B. polymicrodus*”: Fielitz and Shimada, 1999, p. 511); KUVP 283, mandible (Jordan, 1924, p. 221); KUVP 69016 and 69372, partial skull; BMNH P.9202, partial skeleton, BMNH P.9645, P.10158, and P.11147, cranial elements (Taverne, 2004); BMNH P.9646, caudal fin; BMNH P.10610, complete skeleton (Taverne, 2000d).

Notes—This taxon was previously referred to *Anogmius evolutus* and *Bananogmius evolutus* (for review, see Taverne, 2004). Taverne (2001c) suggested that species does not belong to the genus *Bananogmius* and subsequently (Taverne, 2004) placed the species into the genus *Pentanogmius*.

Genus *Bananoanogmius* Loomis, 1900

*Bananoanogmius maltidentatus* Loomis, 1900

Referred material—AMNH FF 994 (lower dental series); KUVP 308, cranial elements; KUVP 309, cranial elements and vertebrae (for review, see Cavin and Forey, 2001).

Notes—The holotype is the only known specimen of this taxon.
Platyceramus platinus (Stewart, 1990b, 1990c, 1996).

Order Crossognathiformes Taverne, 1989
Family Crossognathidae Woodward, 1901
Genus Apsopelix Cope, 1871
Apsopelix anglicus (Dixon, 1850)

Referred material—FHSM 7958, complete skeleton; KUVP 309, complete skeleton; KUVP 310, nearly complete skeleton lacking caudal fin; KUVP 318, head and pectoral girdle; KUVP 519, complete skeleton (Teller-McLarland and Bardack, 1978).

Notes—Synonyms of Apsopelix anglicus are: A. sauriformis Cope, 1871, Syllemaus latifrons Cope, 1875, Pelycorapis bercynicus Cope, 1877a, Leptichthys agilis Stewart, 1899e, Helminthopsis vermiculatus Cockerell, 1919, Placodocupea dakotensis Dante, 1942, and S. hanifi Green, 1957.

Family Pachyrhizodontidae Cope, 1872
Genus Pachyrhizodus Dixon, 1850
Pachyrhizodus caninus Cope, 1872

Referred material—AMNH FF 1658, fragmentary caudal fin (Hussakof, 1908, p. 85); AMNH FF 1662, mandible (Hay, 1903; Nelson, 1973, fig. 2C); AMNH FF 1758 (holotype of Pachyrhizodus latimentum Cope, 1872), mandibles, hyomandibula, and interoperculum; AMNH FF 1881 (holotype), jaw elements; AMNH FF 1900, caudal fin; AMNH FF 1903, vertebrae (Hussakof, 1908, p. 85); AMNH FF 2041, vertebrae and unpaired fin (Nelson, 1973, fig. 8A; Hay, 1903); FHSM VP-2189, skull (Everhart, 2005c, p. 83); KUVP 164, premaxillae; KUVP 278, mandible, unpaired fin (Nelson, 1973, fig. 8A; Hay, 1903); FHSM VP-2189, skull (Everhart, 2005c).

Notes—Synonyms of Pachyrhizodus caninus are: P. caninus (Cope, 1872), partial dentary and vertebrae; CMC VP-7552, incomplete skeleton (Cope, 1877b), partial dentary and vertebrae; CMC VP-7552, complete skeleton (Everhart, 2005c, p. 83); FHSM VP-326 (Miller, 1957; Everhart, 2005c, p. 83); FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); KUVP 62, disarticulated skull and vertebrae; KUVP 2369, caudal fin and vertebrae (Hussakof, 1908, p. 67); AMNH FF 2369, caudal fin and vertebrae; AMNH FF 2522, neurocranium and upper jaws; AMNH FF 3889, premaxilla; AMNH FF 6412, partial neurocranium; AMNH FF 8348, skull fragments and vertebrae; AMNH FF 8363, mandible, partial skeleton (Goody, 1970); FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); KUVP 62, disarticulated skull and vertebrae; KUVP 70, jaws, ceratohyal, and ethmoid; KUVP 71, jaws and ceratohyal (Stewart, 1900); KUVP 59032, pectoral fin, vertebrae, and intestinal cast (Moodie, 1911).

Notes—Synonyms of Cimolichthys nepaholica are: Cimolichthys seminaceps Cope, 1872, C. sulcatus Cope, 1872, Enchodus petrosus Cope, 1874, E. semianceps (Cope, 1872), P. caninus (Cope, 1872), C. seminaceps (Cope, 1872), P. velox (Cope, 1872) and P. leptognathus (Cope, 1872) to be synonyms of P. caninus. Goody (1970) stated that the genus Pachyrhizodus is synonymous with Cimolichthys. Bardack (1965b, p. 9) noted FHSM VP-1649 and VP-5014 as “Cimolichthys sp.” Everhart (2005c, p. 87) noted a “Cimolichthys specimen” (FHSM VP-15065) that contained “a large Enchodus” (FHSM VP-15066) and an unidentified fish (FHSM VP-15067). Everhart (2005c, p. 87) noted also another Cimolichthys specimen (FHSM VP-14024) occurred with an E. petrosus specimen (FHSM VP-14025).

Family Dercetidae Pietet, 1850
Genus Anguillavus Hay, 1903
Anguillavus hackberryensis Martin, 1922

Referred material—KUVP 927 (holotype), complete skeleton (Martin, 1922).

Notes—This taxon was initially described as an anguilliform fish, but Wiley and Stewart (1981) placed it within Dercetidae.

Genus Leptecodon Williston, 1899
Leptecodon rectus Williston, 1899

Referred material—KUVP 35 (holotype), two individuals (Bardack, 1965b, p. 9) noted FHSM VP-1649 and VP-5014 as “Cimolichthys sp.” Everhart (2005c, p. 87) noted a “Cimolichthys specimen” (FHSM VP-15065) that contained “a large Enchodus” (FHSM VP-15066) and an unidentified fish (FHSM VP-15067). Everhart (2005c, p. 87) noted also another Cimolichthys specimen (FHSM VP-14024) occurred with an E. petrosus specimen (FHSM VP-14025).
Genus Stratodus Cope, 1872

Stratodus apicalis Cope, 1872

Referred material—AMNH FF 1753 (holotype), partial skull (Hussakof, 1908, p. 102); KUVP 23, skull with jaws (Stewart, 1900); KUVP 323, partial skeleton (Wiley and Stewart, 1981).

Notes—Churcher (1991) noted the occurrence of this species from the Niobrara Chalk of Kansas (specimens unspecified). Beeson and Shimada (2004) reported this species in a fossiliferous rock specimen curated as FHSM VP-644, but subsequent examination suggests that the material identified as *Stratodus apicalis* is not of the taxon (K. Shimada, unpubl. 2006).

Stratodus oxyrogen Cope, 1877

Referred material—AMNH FF 2113 (holotype), jaws, palatine, and vertebrae (Cope, 1877b; see also Hay, 1903).

Superfamily Enchodontoidea Nelson, 1994

Family Enchodontidae Woodward, 1901

Genus Enchodus Agassiz, 1835

Enchodus dirus (Leidy, 1857)

Referred material—KUVP 322, dentary; KUVP 516, palatine; KUVP 817, skull (Green, 1913).

Notes—Leidy (1857) described this species as *Phasganodus dirus*, but Cope (1875) showed that it belongs to *Enchodus*.

Enchodus gladiolus (Cope, 1872)

Referred material—AMNH FF 1685, partial skull; AMNH FF 1818, partial skull (Hay, 1903); AMNH FF 1820 (holotype of *Enchodus dolichus* Cope, 1875), palatine; AMNH FF 1837, skull; AMNH FF 1865, partial skull (Hussakof, 1908, p. 71, 72); FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); KUVP 174, disarticulated skull; KUVP 808, partial skull; KUVP 812, hyopalatines (Fieltz, 2002); KUVP 814, skull and pectoral fins; KUVP 816, upper jaws and mandible; KUVP 819, disarticulated skull; KUVP 820, disarticulated skull (Green, 1913); KUVP 821, dentary (Stewart, 1900); KUVP 831, disarticulated skull; KUVP 832, mandible, palatines, and premaxilla (Green, 1913).

Notes—Cope (1872) designated *Enchodus gladiolus* as a new species of *Cimolichthys*. *Cimolichthys gladiolus* Cope, 1872, was based on an unnumbered specimen at the AMNH that was lost and has never been recovered (Hay, 1903). *Enchodus dolichus* Cope, 1875 (e.g., see Loomis, 1900), is a synonym of *E. gladiolus* (Green, 1913). The name *E. dolichus* continued to be used (Hay, 1903; McNulty and Kienzlen, 1970) until Goody (1976) reaffirmed it as a synonym.

Enchodus petrosus Cope, 1874

Referred material—AMNH FF 198 (holotype of *Enchodus saevus* Hay, 1903), disarticulated skull; AMNH FF 1605 (holotype of *Teethodus pephredo* Cope, 1874), palatines and part of dentary; AMNH FF 1608 (holotype), neurocranium and palatine; AMNH FF 1668, partial skull; AMNH FF 2062, skull fragments (Hay, 1903; Hussakof, 1908, p. 73); AMNH FF 2098, palatines, jaws, and suspensorium; AMNH FF 2098, partial skull and vertebrae; AMNH FF 8139, palatines; BMNH P9647, skull (Goody, 1976); FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); FHSM VP-2939, skull; FHSM VP-14025, partial skeleton (Everhart, 2005c, p. 85, 87); KUVP 51, mandible and opercle; KUVP 126, palatines (Green, 1913); KUVP 324 (holotype of *E. amicrodus* Stewart, 1898d), dentary (Goody, 1976); KUVP 379, disarticulated skull; KUVP 800, palatine; KUVP 802, palatine; KUVP 803, jaws; KUVP 804, disarticulated skull; KUVP 805, disarticulated cranium; KUVP 806, caudal fin; KUVP 807, complete skeleton; KUVP 833, palatine tooth; KUVP 836, cranium; KUVP 837, palatine; KUVP 839, mandible (Green, 1913).

Notes—Synonyms of this species include: *Enchodus amicrodus* Stewart, 1898d, *E. saevus* Hay, 1903 (according to Goody, 1976), and *Tetheodus pephredo* Cope, 1874 (according to Hay, 1903). Everhart (2005c, fig. 5.3) illustrated three jaw fragments of *E. petrosus* (unnumbered specimens). KUVP 21 is attributed to *E. petrosus* by Green (1913).

Enchodus shumardi Leidy, 1856

Referred material—FHSM VP-644, teeth (the catalogue number is assigned to an entire fossiliferous rock specimen which yielded the teeth: Beeson and Shimada, 2004); KUVP 321 (neotype of *Enchodus parvis* Stewart, 1898d), dentary; KUVP 323, dentary; KUVP 377, dentary, palatal bones, and preopercle; KUVP 823, opercular bones; KUVP 824, dentary; KUVP 825, dentary; KUVP 826, dentary; KUVP 827, skull with jaws; KUVP 828, palatine tooth; KUVP 829, skull; KUVP 838, palatine tooth (Green, 1913).

Notes—*Enchodus parvis* Stewart, 1898d, is a synonym of *E. shumardi* (Loomis, 1900; Green, 1913).

Additional remarks (at genus level)—Fishman, Shimada et al. (1995) and Fishman, Fieltz et al. (1995) referred to FHSM VP-11062 and KUVP 809, respectively, as *Enchodus* from the Smoky Hill Chalk of Kansas, but they did not specify the species. Everhart (2005c, p. 87) discovered “a large *Enchodus*” (FHSM VP-15066) inside a “Cimolichthys specimen” (FHSM VP-15065) along with an unidentified fish (FHSM VP-15067).

Additional remarks (at order level)—Everhart (2005c, p. 99, tables 5.1, 13.1) noted the occurrence of *Apatodus* Woodward, 1901 (superfamily Ichthyotingoidea Nelson, 1994: family incertae sedis) in the Smoky Hill Chalk of Kansas (specimens unspecified; see also Stewart, 1990a, p. 25, 30).

Order Polymixiiformes Rosen and Patterson, 1969

Family Polymixiidae Gill, 1862

Genus Omosoma Costa, 1857

Omosoma garrettii Baradack, 1976

Referred material—AMNH FF 9837, 9838, and 9840, multiple individuals (Baradack, 1976; Stewart, 1990c): FHSM VP-5115, multiple individuals (Stewart, 1990b); FMNH PF3040 (holotype; as “FMNH PF43040” in Stewart, 1990b), skull with jaws; AMNH FF 2113, impression of two individuals (Bardack, 1976; Stewart, 1990c); FHSM VP-5115, multiple individuals (Bardack, 1976; Stewart, 1990c).

Notes—Almost all *Omosoma garrettii* specimens are found on valves of the inoceramid bivalve, *Platyceramus platinus* (Baradack, 1976; Stewart, 1996). Partial individuals of this species have been found associated with and possibly inside the holotype of *Leptocodon rectus* as stomach contents (Stewart 1990b, p. 36, fig. 5, 1990c, p. 57, 1996, p. 390).

Superorder Acanthopterygii Rosen and Patterson, 1969

Order Beryciformes Berg, 1940

Family Holocentridae Richardson, 1846

Genus Kansius Hussakoff, 1929

Kansius sternbergi Hussakoff, 1929

Referred material—FHSM VP-25 (holotype), impression of two individuals (Hussakof, 1929; Bardack, 1965b); FHSM VP-8123, ca. 50 individuals; KUVP 345, multiple individuals (Baradack, 1976).

Notes—Almost all *Kansius sternbergi* specimens are found on valves of the inoceramid bivalve, *Platyceramus platinus* (Baradack, 1976; Stewart, 1996).
Genera and species undetermined

Referred material—AMNH FT 9840, multiple individuals (Stewart, 1990b, 1990c); FHSM VP-2161, individual (Stewart, 1996, p. 390; probably the same material as “SMM 11543” in Bardack, 1976, figs. 7–8); KUVP 27241, multiple individuals?; KUVP 47245, 28 individuals; KUVP 47247, multiple individuals?; KUVP 49403, 104 individuals, KUVP 57251, 65697, 65700, 69467–69483, and 72413–72415, multiple individuals; KUVP 82576, individual; LACM 132681, individual; LACM 131596, individual; USNM 336382–336386, multiple individuals (Stewart, 1990b, 1990c, 1996, p. 390).

Notes—All holocentrid specimens are found on valves of the inoceramid bivalve, Platyceramus platinus (Stewart, 1996). Stewart (1996) noted that FHSM VP-2161 and KUVP 82576 may be conspecific.

Additional remarks (at family level)—Although we cite only one taxon of undetermined genus and species of Holocentridae, Stewart (1990a, 1990b, 1990c, 1996) noted the presence of four undescribed genera of the family Holocentridae. Stewart (1996, p. 390) noted the occurrence of Caproberyx Regan, 1911, and Trachichthysoides Woodward, 1902 (unspeciﬁed species), on valves of the inoceramid bivalve, Platyceramus platinus, from the Smoky Hill Chalk of Kansas.

Order incertae sedis (within Acanthomorpha Rosen, 1973)

Family Ferririnidae Arratia and Chorn, 1998

Genus Ferririons Jordan, 1924

Ferririons rugosus Jordan, 1924

Referred material—KUVP 296 (holotype), anterior half of skeleton (Schultze et al., 1982).

Notes—This taxon is considered to be an acanthomorph fish (Arratia and Chorn, 1998). Part of the holotype (KUVP 296) was found to be a non-Ferririons element, but plethodont material (KUVP 68902; see Arratia and Chorn, 1998, p. 301).

Order incertae sedis

Family incertae sedis

Genus Laminospindus Springer, 1957

Laminospindus transversus Springer, 1957

Referred material—KUVP 312, complete fish (Jordan, 1924, pl. 21; for review, see Schultze et al., 1982).

Notes—KUVP 312 was initially described as Leptichthys agilis by Stewart, 1900, and also followed by Jordan (1924).

Order incertae sedis

Family incertae sedis

Genus Aethocephalichthys Fielitz, Stewart, and Wiffen, 1999

Aethocephalichthys hyainarhinos Fielitz, Stewart, and Wiffen, 1999

Referred material—KUVP 84901, neurocranium (Fielitz et al., 1999).

Subclass Sarcopterygii

Order Coelacanthiformes Lund and Lund, 1985

Family, genus, and species undetermined

Referred material—LACM 131958, partial cranium (Stewart et al., 1991; Everhart, Everhart, and Stewart, 1995; Everhart, 2005c, p. 101; Fig. 2H).

DISCUSSION

Our study shows that the sum of paleoichthyological specimens representing whole or parts of fishes from the Smoky Hill Chalk documented in literature is 643. This represents the sum of all the numbers in parentheses in Table 1 with FHSM VP-644 included separately for each taxon. This figure includes neither specimens discussed in literature without referable catalogue numbers (e.g., many specimens discussed in “Notes” and “Additional remarks”) nor does it include specimens that are catalogued in museums but have never been documented in published papers. It does, however, include the only known specimens (holotypes) of Pseudothryptodus intermedius and Plethodus rotundus that were destroyed during the Second World War. Of the 643 catalogue numbers, 133 belong to chondrichthyans and 510 to osteichthyans.

The 643 described paleoichthyological specimens support the occurrence of a minimum of 70 fish species from the Smoky Hill Chalk of Kansas, comprising at least 16 chondrichthyans and 54 osteichthyans (Table 1). Of these 70 species, 44 are represented by type specimens from the Smoky Hill Chalk. These counts do not include undescribed taxa, such as a number of Stewart’s (1982, 1996, p. 390) holocentrid taxa (including Caproberyx sp. and Trachichthysoides sp.), Everhart’s (2005c, tables 5.1, 13.1) Belonostomus sp. and Apateodus sp., and Shimada’s (unpublished data referred to in Taverne, 2003, p. 170) plethodont taxon. Once these taxa are formally described, the total taxonomic count of non-tetrapod vertebrates would increase if there is no deletion of species from the Smoky Hill Chalk and no synonymization of listed taxa.

In his list of Smoky Hill Chalk vertebrates, Russell (1988, 1993) listed 64 non-tetrapod vertebrate taxa, not counting species of Stewart’s (1982) four undescribed holocentrid genera. Our list includes a number of species not in Russell’s list. For example, the number of known Squalicorax species from the Smoky Hill Chalk is doubled by the addition of S. pristodontus and S. volgensis. However, the increased number of taxa in this paper is not due to a simple addition of previously unreported species. In some instances, the number of species decreased in certain groups. For example, Russell (1988) listed six species of Psychodus, but we removed two species (P. mammillaris and P. occidentalis) as not occurring in the Smoky Hill Chalk and added a species (P. cf. P. latissimus). Russell recorded 16 tselfatiiform species, including seven Martinichthys species. Recent studies of this fish group by Taverne (2000b, 2000c, 2002b) have resulted in the reduction of Martinichthys species to two; however, some previously unreported and new taxa are added to our list (e.g., Plethodus, Pseudanogmius, and Dixonanogmius), which makes the total count of Tselfatiiformes from the Smoky Hill Chalk of Kansas 13 (for summary, see Taverne and Gayet, 2005). Thus, it should be emphasized that the taxonomic composition of certain groups listed by Russell (1988) is quite different from that in our list.

It is noteworthy that the occurrences of 12 of the 16 chondrichthyan taxa and 32 of the 54 osteichthyan taxa in the Smoky Hill Chalk are supported by fewer than ﬁve specimens, and 5 chondrichthyan taxa and 21 osteichthyan taxa are represented by a single specimen each (Table 1). Several of these ‘single-representative taxa’ (by number of catalogued specimens) are newly recognized taxa from the Smoky Hill Chalk, such as Johnlongia sp., Squalicorax volgensis, Rhinobatos sp., and Palaeobalistum sp. It should be noted that these recently added taxa are represented by small (>10 mm) specimens (Fig. 2) collected as a result of paying particular attention to minimizing the collecting bias in the Niobrara fossil record (e.g., see Hamm and Shimada, 2002b).

Böttjer (2002) characterized the Smoky Hill Chalk of Kansas as a fossil Lagerstätte. However, our data suggest that the Niobrara fossil record is manifested with complex multiple effects of preservation, collecting, and research biases. Our personal experiences in the field and in museum collections suggest that, relative to remains of Cretacoryrhina, Squalicorax falcatus, Cimolichthys, and Enchodus petrosus for example, the occurrences of the following fish taxa are simply rare in the Smoky Hill Chalk: Edaphodon, Hadrodus, Lepisosteus, Asaratus, Plethodus, Pseudothyridopterus, Anguillanus, Leptecodon, and coelacanth. Some other fishes, such as Omomura and holocentrids, are also not so common; however, when they are found, these fishes often come in groups, as many as tens of complete or nearly complete, conspeciﬁc individuals preserved together on inoceramid bivalve shells. Their unique mode of preservation and the well-preserved nature of the specimens have attracted some detailed examinations of these fishes (e.g., Bardack, 1976; Stewart, 1990b,
TABLE 1. List of fish taxa from Smoky Hill Chalk of Kansas reported to date. Number in parentheses indicates total specimen count by referable catalogue numbers documented in literature (i.e., sum of specimens listed in “Referred material” for each taxon). Single asterisk (*) denotes count that includes FHSM VP-644, catalogue number assigned to fossiliferous rock specimen that contained the taxon (Beeson and Shimada, 2004). Double asterisk (**) indicates taxon with no representative specimen (i.e., the only known specimen for the taxon is lost).

Chondrichthyes

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Species</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edaphodon sp.</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Ptychodus anonymous</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Ptychodus cf. P. latissimus</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Ptychodus martini</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Ptychodus mortoni</td>
<td>(4)</td>
<td></td>
</tr>
<tr>
<td>Ptychodus polygyrus</td>
<td>(4)</td>
<td></td>
</tr>
<tr>
<td>Scapanorhynchus raphidion</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Johnlongia sp.</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Cretalamma appendiculata</td>
<td>(3)</td>
<td></td>
</tr>
<tr>
<td>Cretoxyrhina mantelli</td>
<td>(47)</td>
<td></td>
</tr>
<tr>
<td>Ptycolocoryx laevis</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Ptycolocoryx falcatus</td>
<td>(32')</td>
<td></td>
</tr>
<tr>
<td>Ptycolocoryx kaupi</td>
<td>(28)</td>
<td></td>
</tr>
<tr>
<td>Ptycolocoryx pristodontus</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Ptycolocoryx volgensis</td>
<td>(1')</td>
<td></td>
</tr>
<tr>
<td>Rhinobatos sp.</td>
<td>(1')</td>
<td></td>
</tr>
</tbody>
</table>

Osteichthyes

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<tr>
<th>Taxon</th>
<th>Species</th>
<th>Number</th>
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</thead>
<tbody>
<tr>
<td>Protosphyraena</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Micropycnodon kansasensis</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Hadrodus marshi</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Palaeobalistum sp.</td>
<td>(1')</td>
<td></td>
</tr>
<tr>
<td>Lepisosteus sp.</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Protosphyraena gladius</td>
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<tr>
<td>Protosphyraena nitida</td>
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<td>Protosphyraena perniciosa</td>
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<tr>
<td>Protosphyraena tenuis</td>
<td>(24)</td>
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<tr>
<td>Paralioideus guadagnini</td>
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<tr>
<td>Asarotus arcanus</td>
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<td>Gillicus arcuatus</td>
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<td>Ichthyodecus ctenodon</td>
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<td>Xiphactinus audax</td>
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<td>Prosaurodon pygmaeus</td>
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<td>Saurocephalus lanciformis</td>
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<tr>
<td>Saurodon leanus</td>
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<tr>
<td>Bananognathia aratus</td>
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</tr>
<tr>
<td>Bananognathia favirratus</td>
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<td></td>
</tr>
<tr>
<td>Lactilites striolatus</td>
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<td></td>
</tr>
<tr>
<td>Syngnathus alatus</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Niobrara encarsia</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>Martinichthys brevis</td>
<td>(3)</td>
<td></td>
</tr>
<tr>
<td>Martinichthys ziphioides</td>
<td>(10)</td>
<td></td>
</tr>
<tr>
<td>Pseudothryptodus intermedius</td>
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<td></td>
</tr>
<tr>
<td>Thrypodus zitteli</td>
<td>(5)</td>
<td></td>
</tr>
<tr>
<td>Plathodon rotundus</td>
<td>(1'')</td>
<td></td>
</tr>
<tr>
<td>Pseudanognathus maiseri</td>
<td>(3)</td>
<td></td>
</tr>
</tbody>
</table>

1990c). In contrast, Protosphyraena and Martinichthys are generally represented only by pectoral fins and rostra, respectively, possibly because other parts of their skeletons were poorly ossified in life. Even though these remains are generally incomplete and occur sparsely isolated in the chalk beds, they are taxonomically easy to diagnose and show paleoecologic and biostratigraphic significance (e.g., Stewart, 1988; Everhart and Everhart, 1993, 1994). Another example of mixed effects of preservation, collecting, and research biases is the case with Cretoxyrhina mantelli. Fourteen of the 47 referred specimens in literature are represented by well-studied nearly complete skeletons, skeletal parts, or associated teeth (e.g., Shimada, 1997c, 1997d). However, our field experience suggests that isolated teeth of the shark are far more common than associated teeth and skeletal remains. Because various biases are apparently operating on each fish taxon at different levels, characterizing the Niobrara fauna as a fossil Lagerstätte may be an overstatement.

Russell (1988) estimated that about 7,416 vertebrate specimens had been recovered from the “Niobrara Chalk” of which approximately 57% (4,222 specimens) are non-tetrapod vertebrates. Whereas our data do not include tetrapod species, we note that counting the number of specimens for each species does not reflect the abundance of any given taxon. Some chondrichthyans are represented by a complete skeleton, associated tooth set, or a set of skeletal parts from an individual (e.g., Shimada, 1997c, 1997d), but the majority of cataloged specimens are isolated teeth. In some cases, one tooth is given a unique catalogue number, whereas other teeth are curated in groups with ‘lot’ numbers corresponding to multiple samples of the same taxon. This situation is not restricted to chondrichthyans. For example, an assemblage of individuals of the same fish species may occur in close proximity (e.g., holocentrid taxa on inosceramid valves: Stewart, 1990b, 1990c), and the entire assemblage, or part of the assemblage, may be given a single catalogue number. In addition, Bardack (1965a) documented the fact that a number of ichthyodectiform specimens are actually composite skeletons (i.e., a reconstructed skeleton consisting of more than one individual fish). Nevertheless, our field experience suggests that fish fossils are far more common than tetrapod fossils in the Smoky Hill Chalk of Kansas. Our intuition is that there is a collecting bias towards large tetrapods, such as mosasaurs, in the Niobrara fossil record, and that the proportion of fish specimens cataloged in museum collections estimated by Russell (1988: i.e., 57%) appears far smaller than the actual proportion of fishes to tetrapods in the field. This is supported by Everhart’s (2005c) account of field collecting. Based on his field notes, fish specimens make up 78% of all specimens collected in a six year period.

The Smoky Hill Chalk was deposited over about five million years (Obradovich and Cobb, 1975, p. 50), but it must be noted that the “Niobrara fauna” is a chronologically mixed (= time averaged) faunal assemblage (Stewart, 1990a; for time-averaging, see Kidwell and Behrensmeyer, 1993), because fossils have been collected from various horizons within the 180-m-thick stratigraphic member. In other words, not all listed species coexisted at any given point of time during the deposition of the Smoky Hill Chalk. For example, Bardack (1965b) noticed that the occurrences of Ptychodus and Protosphyraena are restricted to the lower part of the stratigraphic member, and Stewart (1988) demonstrated that even different species of Protosphyraena have different stratigraphic ranges.
were three major periods of Smoky Hill Chalk paleoichthyological research. Has constantly increased for the last three decades (Fig. 3B). Everhart (2005c). Our historical examination suggests that the amount of research in fish taxa and related biostratigraphy has substantially declined since the end of the nineteenth century and early twentieth century (Fig. 3A). It is intriguing, however, that the amount of research in fish taxa and related biostratigraphy has constantly increased for the last three decades (Fig. 3B).

Our further historical review of literature (Fig. 4) suggests that there were three major periods of Smoky Hill Chalk paleoichthyological research. The first peak in research activity was the decade between 1870 and 1879. The published research at this time period were Cope’s (1870, 1871, 1872, 1873, 1874, 1875, 1877a, 1877b, 1877c, 1878) descriptions of the majority of osteichthyan taxa (Fig. 4). Curiously, no work on the Smoky Hill Chalk fauna seemed to take place during the 1880s with regard to fishes.

The second major period of research activity was between the late 1890s and into the early 1900s (Fig. 4). This period was probably the most productive in the shortest amount of time. Cope’s interest in fishes largely vanished by 1880 based on his publication record (e.g., see “References” below), but new workers such as O. P. Hay, F. B. Loomis, A. Stewart, and S. W. Williston resumed taxonomic work on the fish fauna. In addition to the description of new species, much of this work was a re-examination of Cope’s descriptions of the 1870s. Taxonomic research continued from 1910 until early 1960s, although to a lesser degree than in the past. There was a small peak in the 1920s reflecting an increase in new species descriptions from the Smoky Hill Chalk (e.g., by Jordan, 1924). This is also the time frame when G. F. Sternberg, a prominent fossil hunter (Fig. 1), began to collect fossils from the Niobrara Chalk of Kansas extensively (see Rogers, 1991).

The third major peak in research activity began in about the mid-1960s, but accelerated in the 1970s and is still on the increase today (Fig. 4). This recent resurgence in the study of fish taxa of the Smoky Hill Chalk is likely a reflection of the renewed interest in systematic ichthyology brought on by seminal papers such as Greenwood et al. (1966) and the first Interrelationships of Fishes (Greenwood et al., eds., 1973), as well as the training of new ichthyologists from such institutions as the AMNH and BMNH. Much of the work on the osteichthyan has been centered on re-description of the taxonomic groups and placing them in a phylogenetic context (e.g., Taverne, 1989, 1999, 2000a, 2000b, 2000c, 2001a, 2001b, 2001c, 2002a, 2002b, 2003). Additionally, there has been more work related to biostratigraphy and paleoecology of the Smoky Hill Chalk fishes (e.g., Stewart, 1990a, 1990b, 1999b; Everhart, Everhart, and Shimada, 1995; Everhart, Everhart, and Stewart, 1995; Shimada, 1997e; Everhart, 2005d).

A significant trend in the current explosion of taxonomic research in the Smoky Hill Chalk is an increase in the study of chondrichthyans, (e.g., Shimada, 1997c, 1997d; Hamm, 2001; Everhart and Caggiano, 2004; Shimada and Cicimurri, 2005). Little work was done on this group after Williston (1900a, 1900b). This renewed interest may be due to a rise in collecting in the Smoky Hill Chalk during the past several decades, and an increasing appreciation of the diversity in the chondrichthyan taxa. It can also be attributed to the work of Hattin (1982) and Stewart (1990a) that allowed specimens to be described in a stratigraphic and biostratigraphic context.

CONCLUSION

The Niobrara Chalk of Kansas is said to be “the most-diverse and best-known Mesozoic fish assemblage in North America” (Wilson and Bruner, 2004, p. 583). Our study shows that, although the ichthyofauna constitutes a time-averaged assemblage, there are minimally 70 fish species, comprising at least 16 chondrichthyans and 54 osteichthyan species currently known from the Smoky Hill Chalk of Kansas. It is encouraging that, in recent years, there is renewed interest in systematic ichthyology, biostratigraphy, and paleoecology, concerning Niobrara fishes. However, much work on vertebrate biostratigraphy within the Niobrara Chalk is still needed. It is our belief that progress in future studies of Niobrara fauna depends particularly on two factors. First, collecting bias must be minimized, and second, a “good” record of stratigraphic and locality data must be kept for each collected specimen. Whereas collecting every remaining fossil fishes (including searching and recovering microscopic specimens) and identifying the exact stratigraphic horizon and geographic position in the field may not be easy, such practices would contribute to elucidating a more accurate picture of the paleoecology and evolutionary history of the Niobrara fauna.
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It must be noted that the authors assume the responsibility of the content of this paper, not the reviewers.

Both authors contributed in equal parts to this work. We did our best to provide an exhaustive entrée to the literature on Niobrara fishes; however, if any relevant papers are inadvertently omitted, we would like to learn about such publications. Compilation of publications cited in this work was completed in December of 2005.

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FIGURE 4. Graph showing number of times species were cited per decade of research.
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