

# THE OCCURRENCE OF FOSSIL CARTILAGINOUS FISHES (CHONDRICHTHYES) WITHIN THE PARKS AND MONUMENTS OF THE NATIONAL PARK SERVICE

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**Abstract**—The lands under the jurisdiction of the National Park Service (NPS) have an extensive chondrichthyan (cartilaginous fish) fossil record that spans temporally all the eras of the Phanerozoic and geographically throughout the United States. A total of 46 NPS units have yielded fossil chondrichthyans representing 16 units with specimens from the Paleozoic, sixteen units with specimens from the Mesozoic, and seventeen units with specimens from the Cenozoic. Though there is a rich record of fossil chondrichthyans within the National Park Service, the majority of these assemblages and collections have not yet been fully identified, studied, or published scientifically.

## INTRODUCTION

The class Chondrichthyes, the cartilaginous fishes, is a group of vertebrates with more than four hundred and forty million years of paleobiological history on Earth, with fossils found on every continent. The earliest fossils that can confidently be assigned to chondrichthyans are isolated dermal denticles found in Upper Ordovician and upper Silurian rocks (Ginter et al., 2010). Shark teeth first appear in the fossil record during the Early Devonian (Ginter et al., 2010; Andreev et al., 2016). Chondrichthyan teeth and tooth plates have extensive fossil records through the rest of the Paleozoic and into the Recent (Stahl, 1999; Ginter et al., 2010; Cappetta, 2012; Friedman and Sallan, 2012).

Shark teeth are the most common vertebrate fossils to be collected by both scientist and hobbyist. Many specimens collected by paleontologists working under research and collecting permits have come from public lands such as the parks and monuments of the National Park Service. The following is an overview of the occurrence of chondrichthyan fossils found within National Park Service units throughout the United States (Fig. 1). At least eight fossil chondrichthyan holotype specimens have been described and named from five different NPS units (Table 1). This review was generated by information from peer-review publications, NPS paleontological resources inventories (PRI), and new unpublished data from NPS paleontology research projects.

**Institutional Abbreviations**—**BADL**, Badlands National Park Museum Collections, South Dakota; **CMNH**, Cleveland Museum of Natural History, Cleveland, Ohio; **FOWA**, Fort Washington Park, Maryland; **GRCA**, Grand Canyon National Park, Arizona; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **NATR**, Natchez Trace Parkway, Tupelo, Mississippi; **NMNH/USNM**, National Museum of Natural History, Washington, DC; **PEFO**, Petrified Forest National Park, Arizona; **PISC**, Piscataway Park, Maryland; **SUIT**, Suitland Parkway, Maryland; **YELL**, Yellowstone National Park, Heritage and Research Center, Gardiner, Montana.

## PALEOZOIC

The Paleozoic Era was the apex of chondrichthyan diversity (Zangerl, 1981; Stahl, 1999; Ginter et al., 2010; Friedman and Sallan, 2012). From the Late Devonian (approximately 283 million years ago) to the end of the Permian (approximately 252 million years ago), multiple lineages of chondrichthyans evolved into forms adapted for a diverse range of paleoecological niches (Long, 2010). The greatest height of chondrichthyan diversity occurred during the Late Mississippian, just prior to

the formation of Pangea (Long, 2010). Afterwards, during the Pennsylvanian and Permian species richness of chondrichthyans declined up to the Permian–Triassic Extinction Event, during which many of the major groups of Paleozoic chondrichthyans went extinct (Long, 2010).

Sixteen different NPS units have fossil specimens of Paleozoic chondrichthyans, and these occurrences include the major groups of cartilaginous fishes known primarily from the Paleozoic Era (Fig. 2). Below is a summary of these major Paleozoic chondrichthyan taxonomic groups:

**Symmoriformes**—An order of shark-like chondrichthyans that bear three- to five-cusped teeth on a ovate flattened tooth base (cladodont type); some groups were sexually dimorphic with males having specialized dorsal fin spines bearing denticulated ornamentations (Fig. 2A); known from the Late Devonian to late Permian (Zangerl, 1981; Ginter et al., 2010).

**Cladoselachiformes**—An order of shark-like chondrichthyans with cladodont teeth, a simple dorsal fin spine on the anterior dorsal fin, and sleek bodies with enlarged pectoral fins (Fig. 2A); known primarily from the Late Devonian (Zangerl, 1981; Ginter et al., 2010).

**Phoebodontiformes**—An order of basal, elongate-bodied sharks, some eel-like, with multi-cusped gripping teeth (Figure 2B); known from the Devonian to Late Mississippian (Zangerl, 1981; Grogan and Lund, 2008; Ginter et al., 2010).

**Jalododontiformes**—An order of basal sharks known only from isolated specialized cusped teeth; known from the Late Devonian to Early Triassic (Ginter et al., 2010; Ivanov et al., 2021b).

**Xenacanthiformes**—An order of basal sharks with a single elongate denticulated dorsal fin spine, tricuspid teeth with the lateral cusps larger than the median cusp, and bodies typically elongate (Figure 2C); many freshwater species; known from the Late Mississippian to Late Triassic (Ginter et al., 2010).

**Ctenacanthiformes**—An order of basal sharks with cladodont-like teeth and two dorsal fins bearing dorsal fin spines with denticulate ornamentation (Fig. 2D); sister-group to the Euselachii; known from the Late Devonian to late Permian (Ginter et al., 2010; Hodnett et al., 2021).

**Euselachii**—An infraclass of sharks that include the orders of the Protacrodontiformes, Hybodontiformes, and Neoselachii, (Fig. 2E), as well as a number of miscellaneous taxa (Ginter et al., 2010).

**Protacrodontiformes**—An order of basal euselachian sharks with two large dorsal fin spines and teeth usually with blunt generalized cusps; known from the Late Devonian to Late Mississippian (Ginter et al., 2010).

**Hybodontiformes**—An order of basal euselachian sharks

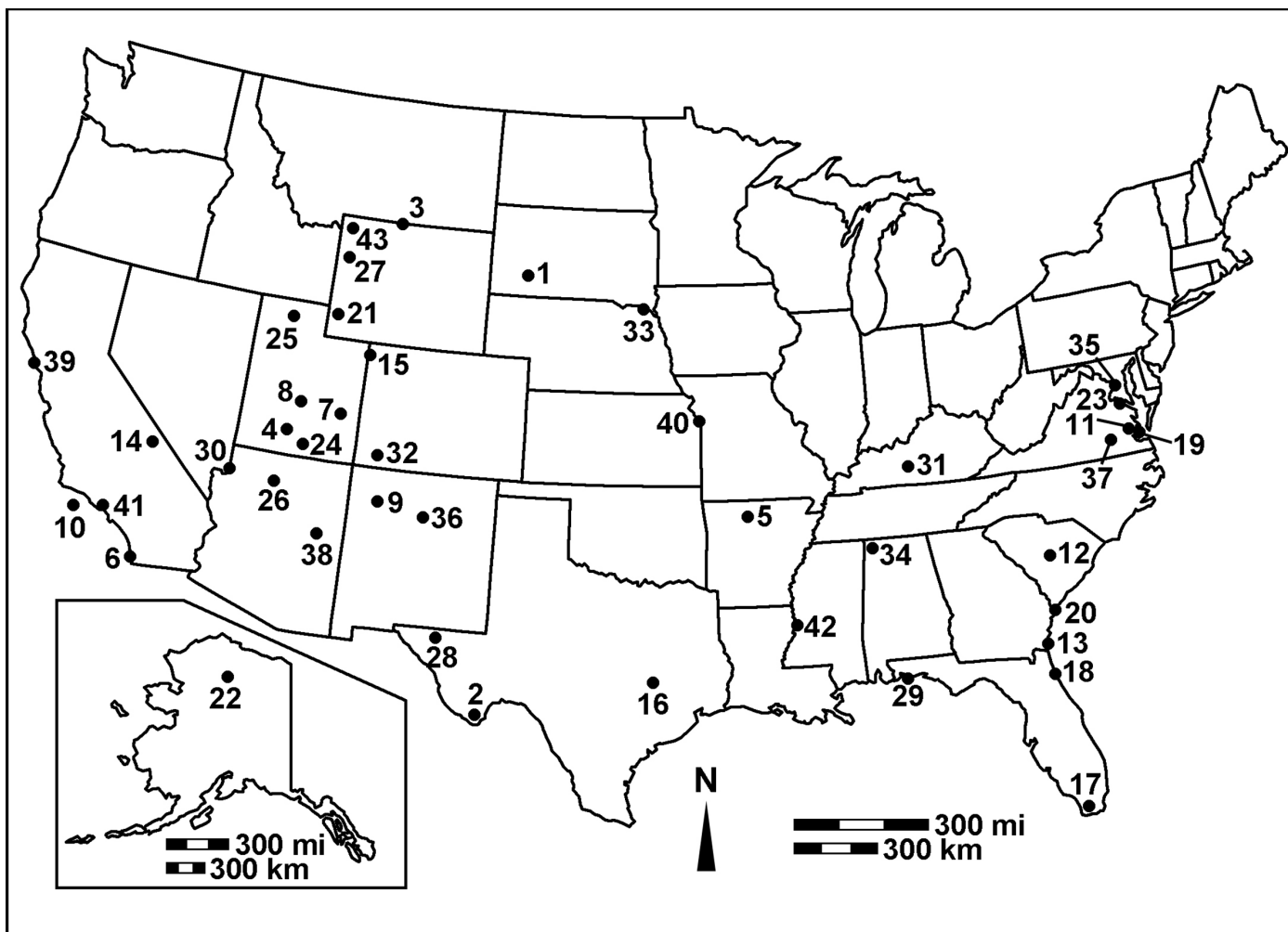


FIGURE 1. National Park Units with fossil shark records: 1. **BADL**, Badlands National Park, South Dakota, 2. **BIBE**, Big Bend National Park, Texas, 3. **BICA**, Bighorn Canyon National Recreation Area, Montana, 4. **BRCA**, Bryce Canyon National Park, Utah, 5. **BUFF**, Buffalo National River, Arkansas, 6. **CABR**, Cabrillo National Monument, California, 7. **CANY**, Canyonlands National Park, Utah, 8. **CARE**, Capitol Reef National Park, Utah, 9. **CHCU**, Chaco Culture National Historical Park, New Mexico, 10. **CHIS**, Channel Islands National Park, California, 11. **COLO**, Colonial National Historical Park, Virginia, 12. **CONG**, Congaree National Park, South Carolina, 13. **CUIS**, Cumberland Island National Seashore, Georgia, 14. **DEVA**, Death Valley National Park, Nevada and California, 15. **DINO**, Dinosaur National Monument, Colorado and Utah, 16. **ELTE**, El Camino Real de los Tejas National Historic Trail, California, 17. **EVER**, Everglades National Park, Florida, 18. **FOMA**, Fort Matanzas National Monument, Florida, 19. **FOMR**, Fort Monroe National Monument, Virginia, 20. **FOPU**, Fort Pulaski National Monument, Georgia, 21. **FOBU**, Fossil Butte National Monument, Wyoming, 22. **GAAR**, Gates of the Arctic National Park and Preserve, Alaska, 23. **GEWA**, George Washington Birthplace National Monument, Virginia, 24. **GLCA**, Glen Canyon National Recreation Area, Arizona and Utah, 25. **GOSP**, Golden Spike National Historic Park, Utah, 26. **GRCA**, Grand Canyon National Park, Arizona, 27. **GRTE**, Grand Teton National Park, Wyoming, 28. **GUMO**, Guadalupe Mountains National Park, Texas, 29. **GUIS**, Gulf Islands National Seashore, Florida, 30. **LAKE** (and **PARA**), Lake Mead National Recreation Area, Nevada and Arizona, 31. **MACA**, Mammoth Cave National Park, Kentucky, 32. **MEVE**, Mesa Verde National Park, Colorado, 33. **MNRR**, Missouri National Recreational River, Nebraska and South Dakota, 34. **NATR**, Natchez Trace Parkway, Mississippi, Alabama, and Tennessee, 35. **NACE** National Capital Parks-East, Maryland, including: (Fort Washington Park [FOWA], Piscataway Park [PISC], Suitland Parkway [SUIT]), 36. **PECO**, Pecos National Historical Park, New Mexico, 37. **PETE**, Petersburg National Battlefield, Virginia, 38. **PEFO**, Petrified Forest National Park, Arizona, 39. **PORE**, Point Reyes National Seashore, California, 40. **SAFE**, Santa Fe National Historic Trail, Colorado, Kansas, Missouri, New Mexico, and Oklahoma, 41. **SAMO**, Santa Monica Mountains National Recreation Area, California, 42. **VICK**, Vicksburg National Military Park, Mississippi, 43. **YELL**, Yellowstone National Park, Wyoming, Montana, and Idaho.

FIGURE 2 (facing page). Representations of Paleozoic chondrichthyans found at National Park Service units. **A)** Cladoselachiformes (*Cladoselache*) and Symmoriiformes (*Stethacanthus* and *Falcatus*). **B)** the Phoebodontiformes with *Phoebodus* and *Thrinacodus*. **C)** the Xenacanthiformes with *Xenacanthus*. **D)** the Ctenacanthiformes with *Saivodus* and *Glikmanius*. **E)** Euselachii with the Neoselachii, *Amaradontus*, the Sphenacanthidae *Wodnika*, the Hybodontidae *Lissodus*, the Protacrodontidae *Microklomax*. **F)** the Paraselachii *Deeberius* and *Heteropetalodus*. **G)** the Orodontiformes *Orodus* and the Eugenodontiformes *Sinohellicoprion*. **H)** the Petalodontiformes with *Petalodus*, *Janassa*, *Obruchevodus*, *Petalorhynchus*, and *Chomatodus*. **I)** the Holocephali with *Helodus*, *Chondrenchelys*, and *Deltoptychius*. Chondrichthyans not drawn to scale between groups.

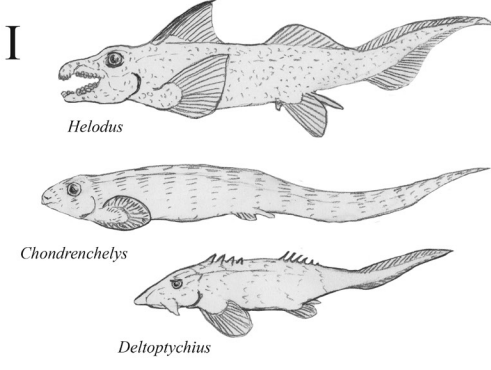
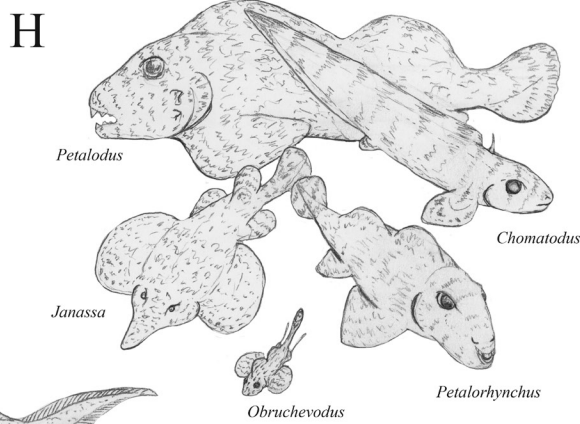
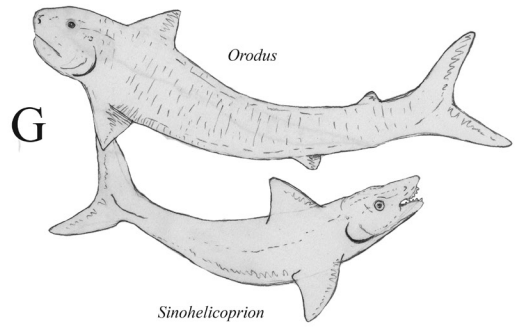
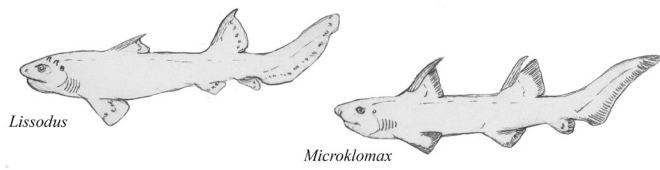
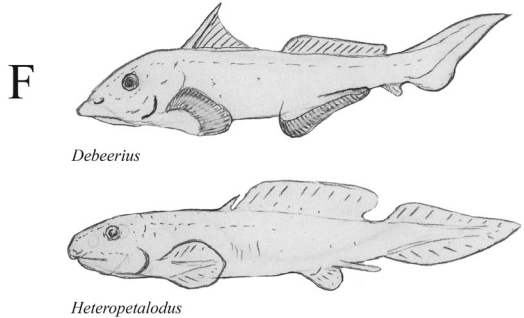
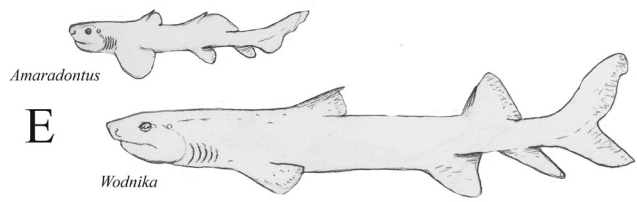
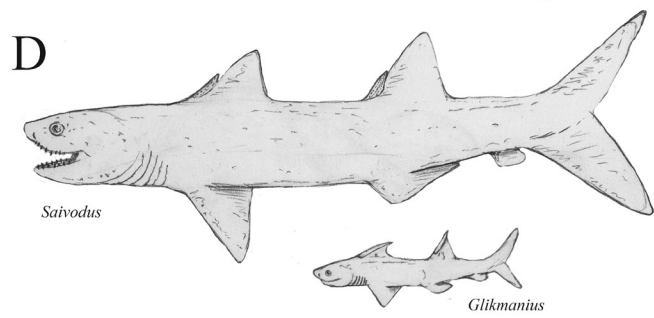
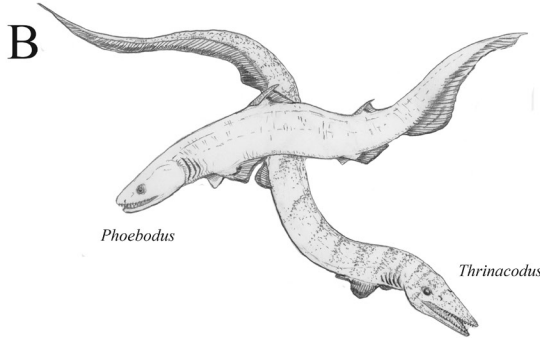
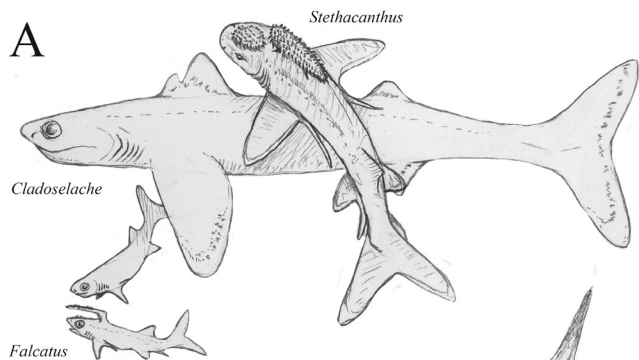


TABLE 1. Type specimens of fossil chondrichthyans from NPS units.

NPS unit	Taxon	Reference	Geologic age and formation	Specimen #	Taxonomic designation
BRCA	<i>Columbusia deblieuxi</i>	Kirkland et al. 2013	Late Cretaceous, Wahweap Fm.	UMNH VP 18878	Scelerorhynchid batoid
BRCA	<i>Texatrygon brycensis</i>	Kirkland et al. 2013	Late Cretaceous, Wahweap Fm.	UMNH VP 18885	Ptychotrygonid batoid
FOBU	<i>Xiphotrygon acutidens</i>	Cope 1879	Eocene, Green River Fm.	Missing MCZ specimen	Ray, now considered a synonym of <i>Heliobatis radians</i>
FOBU	<i>Palaeodasybatis discus</i>	Fowler 1947	Eocene, Green River Fm.	ANSP 8344 (lost; stolen per note at ANSP)	Ray, now considered a synonym of <i>Heliobatis radians</i>
FOBU	<i>Heliobatis radians</i>	Marsh 1877	Eocene, Green River Fm.	YPM 528	Freshwater ray
GRCA	<i>Megactenopetalus kaibabanus</i>	David 1944	Permian, Kaibab Fm.	MNA G2.2280	Pristodontiform euchondrocephalan
GUMO	<i>Lamarodus triangularis</i>	Ivanov et al. 2020	Permian, Bell Canyon Fm.	NMMNHS P-77369 (GUMO 44679)	Hybodont shark
PEFO	<i>Palaeoxyris humblei</i>	Fischer et al. 2010	Triassic, Chinle Fm.	PEFO 34350A (counterpart PEFO 34350B)	Hybodont shark egg capsule

with males bearing specialized hook-like denticles on the sides of their heads, two dorsal fin spines with longitudinal ridges, and teeth either durophagous or grasping in morphology; known from the Early Mississippian to the Late Cretaceous (Ginter et al., 2010). Most Paleozoic hybodonts were small until the Permian (Ginter et al., 2010; Cappetta, 2012).

**Neoselachii**—A division of euselachian sharks that includes all extant sharks and rays, known from the Late Mississippian to present (Ginter et al., 2010; Cappetta, 2012). The oldest neoselachian family is the Anachronistidae, which first appeared during the Late Mississippian (Ginter et al., 2010).

**Paraselachii**—An infraclass of basal shark-like euchondrocephalan chondrichthyans with narrow cusped teeth on elongated tooth bases, some with a single dorsal fin spine (Fig. 2F); known from the Late Devonian to the Late Mississippian (Grogan and Lund, 2000; Lund and Grogan, 2004; Ginter et al., 2010).

**Orodontiformes**—An order of euchondrocephalans with small crushing teeth, elongate bodies, and short blunt heads (Fig. 2G); known from the Late Devonian to the Late Pennsylvanian (Zangerl, 1981; Ginter et al., 2010).

**Eugenodontiformes**—An order of euchondrocephalans with a specialized enlarged lower symphyseal tooth whorl at the anterior of the lower jaw and small crushing lateral teeth (Fig. 2G); known from the Late Mississippian to the Early Triassic (Zangerl, 1981; Ginter et al., 2010; Cappetta, 2012).

**Petalodontiformes**—An order of euchondrocephalans with petal-like to blade-like teeth, bodies ranging from skate-like forms to boxfish-like forms, and all species bearing enlarged flexible pectoral fins (Fig. 2H); known from the Early Mississippian to the late Permian (Ginter et al., 2010; Lund et al., 2014).

**Holocephali**—An infraclass of euchondrocephalans that contains all extant and extinct orders of ratfish; chondrichthyans with the palatoquadrate fused to the neurocranium and the posterior dentition consisting of shearing and crushing dental plates (Fig. 2I); known from the Late Devonian to present (Stahl,

1999). Many of the extinct orders ranged from eel-like forms to low-bodied benthic forms (Stahl, 1999).

### **Bighorn Canyon National Recreation Area, Montana and Wyoming (BICA)**

#### **Late Mississippian**

*Madison Group*—Santucci et al. (1999) noted the presence of crushing teeth belonging to a coeliodont holocephalan in the Madison Limestone of BICA. These tooth plates were originally erroneously placed in the genus *Hybodus*, a hybodont taxon known only from the Mesozoic.

#### **Buffalo National River, Arkansas (BUFF)**

#### **Mississippian**

*Boone Formation* — Indeterminate Mississippian chondrichthyan teeth have been reported from Boone Formation outcrops along the Buffalo River at BUFF (Bitting, personal commun., 2001; Santucci et al., 2001).

#### **Canyonlands National Park, Utah (CANY)**

#### **Late Pennsylvanian to Early Permian**

*Elephant Canyon Formation/Halgaito Formation*—Sumida et al. (1999) reported the occurrence of xenacanth shark teeth from the Elephant Canyon/Halgaito Formation transition just to the northeast of CANY. Lohman (1974) reported the teeth of the chondrichthyans *Deltodus* and *Petalodus* from a red bed site near Shafer Dome in northeastern CANY. Two *in situ* exposed ctenacanthiform spines are reported by NPS staff from within CANY but has not yet been identified beyond order.

#### **Capitol Reef National Park, Utah (CARE)**

#### **Early Permian**

*Cutler Group*—There are reports (Graham, 2006) of possible chondrichthyan teeth from the Cutler Group of Capitol Reef National Park (CARE). The teeth have not yet been identified.

## Death Valley National Park, California and Nevada (DEVA)

### Late Devonian

*Lost Burro Formation*—A small cladodont shark tooth and a cochlodont crushing tooth have been reported from the Lost Burro Formation of DEVA (Dunkle and Lane, 1971). The chondrichthyan specimens are curated at the Cleveland Museum of Natural History, in Cleveland Ohio. Dunkle and Lane (1971) described the cladodont-grade tooth (CMNH 8233) as being small and having only a single set of small lateral cusps. The holocephalan tooth plate was only identifiable based on its histology and was not diagnosable to a genus (Dunkle and Lane, 1971). The cladodont tooth could represent a number of Devonian taxa such as a cladoselachian, a stethacanthid, or a ctenacanthiform (Ginter et al., 2010), while the holocephalan is a unique record as most true holocephalans are rare during the Devonian (Stahl, 1999). Both of these specimens warrant further investigation and suggest that further field work in the Lost Burro Formation may produce other fish specimens.

### Late Mississippian

*Mexican Spring Formation*—A single tooth (NMNH V23108) of a basal euselachian, *Carcharopsis wortheni*, was collected from the Mexican Spring Formation at Rest Spring in 1963 and was deposited in the National Museum of Natural History. The DEVA tooth is the westernmost occurrence of *Carcharopsis wortheni* in North America and is the first Late Paleozoic vertebrate to be described in detail (Hodnett et al., this volume). The Perdido Group at DEVA also has a rich invertebrate fossil assemblage (Nyborg and Santucci, 1999).

*Indian Springs Formation*—Stone et al. (2014) figured a nearly complete ctenacanthiform spine from the Marble Canyon region of DEVA in the Indian Springs Formation. The Indian Springs Formation is a Late Mississippian (Late Chesterian/Serpukhovian) unit of sandstones, shales, and minor limestone that form a general red-weathering recessive interval between the more resistant limestone of the Bird Spring Formation units above and the Santa Rosa Limestone below (Stone et al., 2014).

## Gates of the Arctic National Park & Preserve, Alaska (GAAR)

### Permian

*Siksikpuk Formation*—Santucci et al. (1995) reported the occurrence of Permian chondrichthyan teeth along the Nigu River in Gates of the Arctic National Park and Preserve (GAAR). A shark dorsal fin spine of *Wodnika borealis*, an early euselachian with durophagous teeth, was also collected from the Point Hope region in the Siksikpuk Formation (Maisey, 1982).

## Golden Spike National Historic Site, Utah (GOSP)

### Pennsylvanian

*Oquirrh Formation*—Two teeth of indeterminate chondrichthyans were noted from the Oquirrh Formation within the boundaries of GOSP (Tweet, et al., 2012). Chondrichthyan fossils have also been recovered from conodont residues elsewhere in the Oquirrh Formation in central Utah (Chamberlain and Clark, 1973).

## Grand Canyon National Park, Arizona/Lake Mead National Recreation Area, Nevada (GRCA/LAKE)

Grand Canyon National Park (GRCA) in northern Arizona hosts an extensive physical record of geologic deep time, representing significant portions of the Precambrian and Paleozoic. At least six formations, representing the Mississippian to the early Permian, have produced chondrichthyan body fossils in the park (Hodnett and Elliott, 2021; Fig. 3.). Lake Mead National Recreation Area (LAKE), which continues along the Colorado River west of GRCA in Arizona and Nevada, includes a similar Paleozoic section with a more open marine setting

in the Pennsylvanian and Permian. Both GRCA and LAKE are presented together in this summary as they share the same geologic horizons across NPS administrative boundaries which have been adjusted over time.

### Mississippian

*Redwall Limestone*—The Redwall Limestone is a prominent cliff-forming unit within GRCA, made up of Early to Late Mississippian marine sediments that were deposited during two marine transgression and regression events (McKeen and Gutschick, 1969). McKee and Gutschick (1969), with the help of David Dunkle, were the first to report on marine vertebrate fossils from Redwall Limestone sites within and outside of GRCA. These included a tooth plate from the Kaibab Trail that McKee and Gutschick (1969) originally assigned to *Helodus* sp. Hodnett et al. (2021) examined this specimen and determined that it was, in fact, a posterior tooth plate of *Psephodus* sp. (Fig. 3A). During a later survey, George Billingsley collected a tooth whorl with two teeth belonging to *Helodus* sp. in the Surprise Canyon region of GRCA (Fig. 3B). This specimen was described by Hodnett et al. (2021). All Redwall Limestone vertebrate material from within and outside of GRCA comes from the Mooney Falls Member which is tentatively assigned a Viséan age (McKee and Gutschick, 1969; Hodnett et al., 2021).

*Surprise Canyon Formation*—The Surprise Canyon Formation represents a series of channel fills and karstic cave deposits that were cut into the Redwall Limestone during the Late Mississippian (Serpukhovian). This formation tracks a slow marine transgression and shows its effects on the marine vertebrate community. The vertebrate assemblages were identified in conjunction with an analysis of conodonts. At least seven localities pertaining to three distinct members were found to produce both vertebrate microfossils (1 millimeter or less) and macrovertebrate fossils (Billingsley and Beus, 1999; Hodnett and Elliott, 2018). Hodnett and Elliott (2018) identified thirty-one distinct chondrichthyan taxa from GRCA and adjoining areas, based primarily on isolated teeth. These taxa include the eel-like *Thrinacodus gracia*, the marine xenacanth *Bransonella nebraskensis*, at least four symmoriiform taxa (*Denaeva williamsi*, two indeterminate falcated taxa, and an indeterminate stethacanthid), and the enigmatic elasmobranch *Clairina* sp., a taxon known from the Late Devonian of Africa and Europe (Derycke, 1992; Ginter, 1995). At least three ctenacanthiform taxa have been identified: *Cladodus* cf. *C. marginatus*, cf. *Glencartius costellatus*, and an indeterminate form. Euselachians were particularly diverse for the Late Mississippian and included four new taxa in GRCA (*Microklomax carrieae*, *Novaculodus billingsleyi*, *Cooleyella platera*, *Amaradontus santuccii* [Fig. 3D]), as well as *Cooleyella fordii*, cf. *Mesodmodus* sp., and cf. *Hamiltonichthys* sp.

The euchondrocephalan component of the Surprise Canyon Formation is diverse. The gregoriid *Srianta* cf. *S. srianta* and the debeeriid *Heteropetalus* sp. are two basal euchondrocephalan taxa not previously identified outside of the Bear Gulch Limestone of the Heath Formation in Montana, a fauna that preserves chondrichthyans and other vertebrates in exquisite detail (Lund, 1977; Lund and Grogan, 2004). An indeterminate orodontiform and a caseodontoid eugenodontiform are known from the middle member of the Surprise Canyon Formation at GRCA. Petalodonts are represented by a small tooth fragment from a small indeterminate taxon. Holocephalans are diverse in the Surprise Canyon Formation assemblage with *Helodus* sp., *Cochliodus* cf. *C. contortus* (Fig. 3C), *Deltodus* cf. *D. angularis*, *Deltodus* cf. *D. cingulatus*, and *Deltodus* sp. identified. Though most of the diversity of the Surprise Canyon chondrichthyan assemblage is based on teeth, fragmentary spines of *Acondylacanthus* sp. and *Amelacanthus* sp. were also observed (Hodnett and Elliott, 2018). Hodnett and Elliott (2018) also

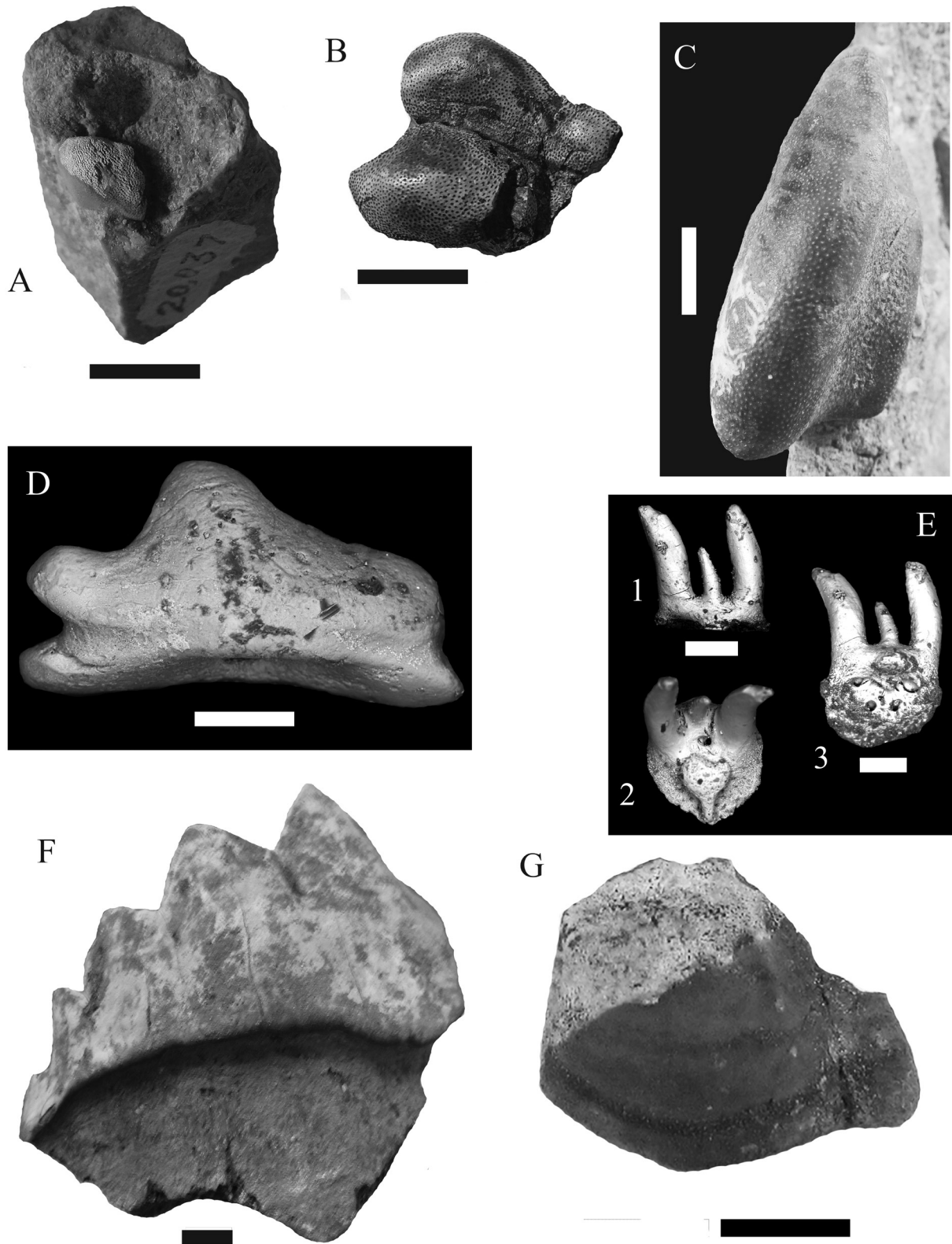


FIGURE 3. Representative Paleozoic chondrichthyan fossils from Grand Canyon National Park, Arizona. **A-B**) chondrichthyan fossils from the Middle Mississippian Redwall Limestone, **A**) GRCA 20037, *Psephodus* sp. tooth plate, **B**) GRCA 121976, *Helodus* sp. tooth whorl. **C-D**) chondrichthyan fossils from the Late Mississippian Surprise Canyon Formation, **C**) USNM PAL412147, *Cochliodus* cf. *C. contortus*, **D**) MNA V11315, *Amaradontus santucci*. **E**) the holotype, MNA V11264, of *Hokomata parva*, tooth from the Early Pennsylvanian Watahomigi Formation; **E1**) labial, **E2**) oral; **E3**) aboral views. **F-G**) chondrichthyan fossil from the Early Permian Kaibab Formation, **F**) the holotype, MNA V1367, of *Megactenopetalus kaibabanus*, tooth **G**) GRCA 9368, *Deltodus mercurii*, tooth plate. Scale bars A-C, F-G scale equals 1 cm; D-E scale equals 200  $\mu$ m.

recognized faunal distinctions between the lower, middle, and upper members of the Surprise Canyon Formation. There was a greater diversity of euselachian sharks in the more coastal to estuarine lower member, a greater total number of chondrichthyan taxa including the occurrence of symmoriiform chondrichthyans in the embayment middle member, and larger though less diverse chondrichthyans in the more open water upper member. In terms of the east-west distribution of chondrichthyans, Hodnett and Elliott (2018) noted that the falcetid symmoriiform chondrichthyans had a distinct distribution pattern in which *Denaea williamsi* was more prevalent in the eastern collection sites representing shallower waters, while the falcetid indet. 1. taxon was found only in the western sections of the Surprise Canyon Formation which represent deeper waters.

### Pennsylvanian

**Watahomigi Formation**—The Watahomigi Formation is the lowest member of the Supai Group and is the Early Pennsylvanian (Bashkirian) continuation of the transgression event that eventually filled the paleovalley system represented by the Surprise Canyon Formation in the Late Mississippian. McKee (1982) was the first to report on the presence of holocephalan tooth plates referable to *Deltodus* from the Grand Canyon. Martin (1992) and Martin and Barrick (1999) also reported the occurrence of micro chondrichthyan fossils from within conodont residue they were evaluating. Hodnett and Elliott (2018) reported two chondrichthyans from the Watahomigi Formation: the small new marine xenacanth *Hokomata parva* (Fig. 3E) and an isolated tooth plate of *Deltodus* sp.

**Wescogame Formation**—The Wescogame Formation is a younger marine transgression event in the Supai Group. McKee (1982) reported isolated tooth plates of *Deltodus* from the Wescogame Formation from both GRCA and LAKE. However, these holocephalan tooth plates are not known to be curated into any museum collection (Hodnett and Elliott, 2021).

### Permian

**Pakoon Limestone**—The Pakoon Limestone is the western lateral equivalent to the Esplanade Sandstone and consists of thick-bedded dolomitic limestones that intertongue with the sandstone unit (McKee, 1982). McKee (1982) reported the occurrence of tooth plates of *Deltodus* sp. and teeth of “*Cladodus* sp.” in LAKE. Hodnett and Elliott (2021) have argued that the “*Cladodus* sp.” must represent another ctenacanthiform taxon as the genus does not extend past the Late Mississippian (Duffin and Ginter, 2006). Neither taxon from the Pakoon Limestone from LAKE is represented in a museum collection (Hodnett and Elliott, 2021).

**Kaibab Formation**—The marine limestone of the early Permian Kaibab Formation historically produced the first record of chondrichthyans for GRCA. The Kaibab Formation is divided into two members, the Fossil Mountain Member and overlying Harrisburg Member (Hopkins and Thompson, 2003). McKee (1938) briefly touched on three chondrichthyan teeth collected from the alpha member (now Harrisburg Member) of the Kaibab Limestone by C.D. Walcott in 1882. Unfortunately, McKee did not offer any taxonomic identification for these three teeth and they are now lost. McKee (1938) did however mention and figure the first chondrichthyan fossil documented from GRCA, a tooth plate of *Deltodus mercurii* (Fig. 3G) collected from an area now called the Fossil Mountain Member near the Desert View visitor center. David (1944) described a new petalodontiform, *Megactenopetalus kaibabanus* (Fig. 3F), from a large upper tooth reportedly collected near Point Sublime on the North Rim of the Grand Canyon. A second, undescribed large tooth plate of *Psephodus* sp. was also collected with or near the *Megactenopetalus* type specimen (Gass, 1963; Hodnett and Elliott, 2021). Thompson (1995) described a number

of small teeth and dermal denticles from several different chondrichthyan taxa from the Fossil Mountain type section at the South Rim of GRCA. The teeth included an indeterminate hybodont, a species close to *Polyacrodus*, and teeth of the early neoselachian *Cooleyella peculiaris* (Thompson, 1995; Hodnett et al., 2011). Thompson (1995) also referred teeth to *Symmorium reniforme*, which Hodnett and Elliott (2021) later referred to the ctenacanthiform *Heslerodus divergens*. Thompson (1995) also identified a number of isolated dermal and buccal membrane denticles of chondrichthyans such as *Cooperella striatolata*, *Sturgenonella quinqueloba*, *Moreyella typicalis*, *Kirkella typicalis*, and a *Petrodus*-like taxon. These denticles are often associated with multiple family groups of chondrichthyans including hybodonts, petalodonts, symmoriids, and holocephalans.

Recently in 2019, the lead author (JPH) along with GRCA staff undertook field surveys on the North Rim inventorying for new vertebrate localities within the Kaibab Formation at Grand Canyon. Two new fossil localities were identified that have produced teeth of the marine xenacanth *Bransonella tribula*, ctenacanthiforms *Glikmanius occidentalis*, *Glikmanius myakhovenski*, and *Neosaivodus flagstaffensis*, at least two indeterminate hybodontiforms, a large indeterminate petalodont, a helodontiform holocephalan, and the holocephalan *Crassidonta stuckenbergi*, which is a new taxonomic record for the Kaibab Formation as a whole.

### Grand Teton National Park, Wyoming (GRTE)

#### Mississippian

**Madison Limestone**—Though no specific chondrichthyan taxa have been identified from the Madison Limestone within Grand Teton National Park (GRTE), sites near the park have yielded fish teeth and tooth plates from the Cottonwood Canyon Member (Benson, 1966) and the Lodgepole Limestone Member of the Madison Limestone (Gutschick et al., 1961; Gutschick and Lamborn, 1975). There is a high probability that these records are of chondrichthyans, and similar fossils may be found in the same beds within GRTE.

**Amsden Formation**—Similarly, specific chondrichthyan taxa have not yet been identified from the Amsden Formation of GRTE. However, Sando et al. (1975) reported on rich chondrichthyan assemblages in close proximity to GRTE from the Moffat Trail and Ranchester Limestone members that include *Cladodus*, “*Pristicladodus*”, “*Lambdodus*”, *Thrinacodus*, “*Stemmatodus*”, *Deltodus*, *Psephodus*, and *Psammodus*.

#### Permian

**Phosphoria Formation**—Yochelson and Van Sickle (1968) noted a number of Permian fish remains from the Forellen Peak region of GRTE. They listed the presence of the ctenacanthiforms “*Cladodus* sp.” and “*Ctenacanthus* sp.”, the eugenodont *Helicoprion* sp., the petalodont *Janassa* sp., the holocephalans *Helodus* sp., *Deltodus* sp., and *Crassidonta* sp., and the enigmatic taxa *Dolophonodus* sp., *Ancistriodus* sp., and *Hamatus* sp. (Yochelson and Van Sickle, 1968). The *Helicoprion* sp. specimen (NMNH V235393, Fig. 4B), a complete symphysial whorl, was recently re-diagnosed as the first North American occurrence of *Sinohelicoprion*, a Permian edestid eugenodontiform previously known only from Chinese deposits (Tapanila et al., 2020).

### Guadalupe Mountains National Park, Texas (GUMO)

#### Permian

**Bell Canyon Formation**—Bell and Polycyn (2011) reported semi-articulated tooth plates and cartilaginous structures of a holocephalan found in the Lamar Limestone Member of the Bell Canyon Formation at GUMO, a unit representing deep-water deposition at the foot of the Capitan Reef. The specimen bears three distinct tooth plate morphologies, from small rhomboidal

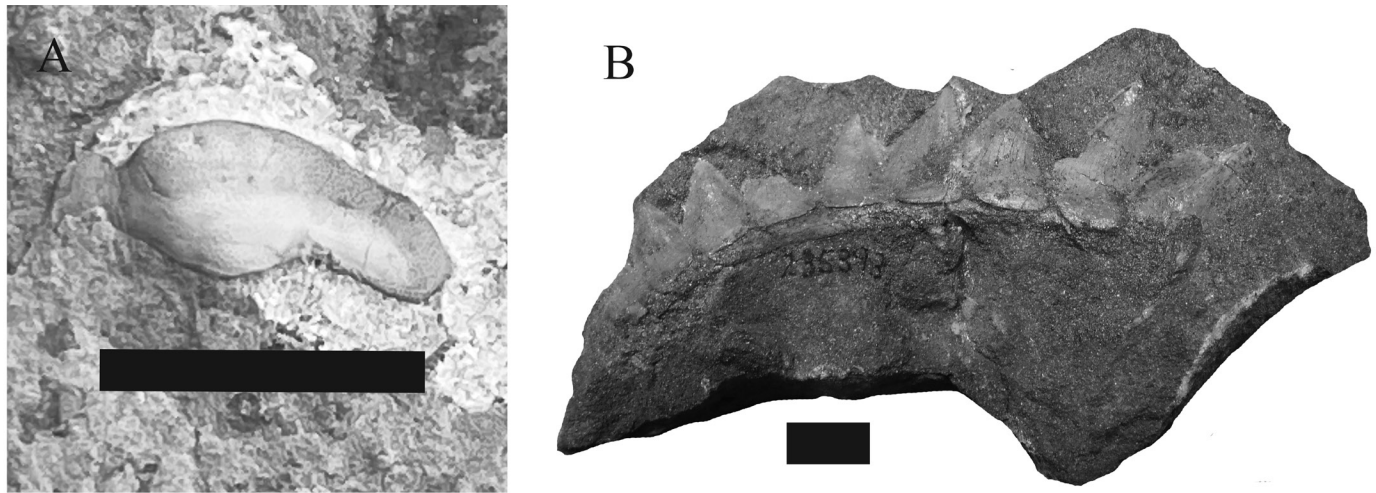


FIGURE 4. Sample of chondrichthyan fossils from Yellowstone and Grand Teton National Parks. A) YELL 133374, a tooth of *Helodus* cf. *H. didymus* from the Madison Limestone at Yellowstone National Park. B) NMNH V235393, the symphyseal tooth whorl of *Sinohelicoprion* sp. from the Phosphoria Formation at Grand Teton National Park, Wyoming. Scale equals 1 cm.

tooth plates to large square and elongated rectangular forms (Bell and Polycyn, 2011). The teeth show resemblance to members of the holocephalan order Psammodontiformes, particularly to the genus *Lagarodus*, but have a unique crown ornamentation and may represent a new taxon (Bell and Polycyn, 2011). Ivanov et al. (2015b) noted the occurrence of the ctenacanth *Glikmanius myachovenski*, the jalodontid *Texasodus* sp., a possible new anachronistid neoselachian, a possible new petalodont similar to *Netsepoye*, and a psephodontid holocephalan. Ivanov et al. (2020) updated this assemblage with *Stethacanthulus meccaensis*, *Texasodus varidentatus*, *Cooleyella* cf. *C. amazonensis*, *Cooleyella* cf. *C. peculiaris*, and a new genus of hybodontiform, *Lamarodus triangulus*.

Just outside of GUMO, Ivanov et al. (2015a) reported the occurrence of the small falcated symmoriiform *Stethacanthulus meccaensis*, the jalodontid *Texasodus varidentatus*, a basal hybodontiform similar to *Polyacrodus*, the anachronistid neoselachian *Cooleyella duffini*, and miscellaneous chondrichthyan denticles from the Rader Limestone Member of the Bell Canyon Formation from a road cut (“Rader Slide”) just south of Bell Canyon.

**Cherry Canyon and Brushy Canyon formations**—Ivanov et al. (2015b) reported the occurrence of a diverse chondrichthyan assemblages with similar taxa from both the Pipeline Shale of the Cherry Canyon Formation and the Getaway Member of the Bushy Canyon Formation. This assemblage includes the symmoriids *Stethacanthulus meccaensis*, *Stethacanthulus decorus*, *Stethacanthus* sp., the ctenacanths *Glikmanius myachovenski*, *Glikmanius occidentalis*, *Heslerodus divergens*, cf. *Tamiobatis* sp., cf. *Cladodus* sp., the hybodonts *Acrodus sweetlacruzensis* and *Lissodus* sp., an indeterminate eugenodont, and a cochlodontid holocephalan (Ivanov et al., 2015b).

**Cutoff Formation**—Ivanov et al. (2015b) reported several teeth, scales, denticles, and other dermal elements, including a possible new genus related to the euselachian *Gissarodus*, from the Shumard and El Centro members of the Cutoff Formation within GUMO. Additional taxa include *Stethacanthulus meccaensis*, an indeterminate symmoriid, the ctenacanth *Glikmanius occidentalis*, *Heslerodus divergens*, *Tamiobatis* sp., *Cladodus* sp., and a hybodontiform similar to *Lissodus* (Ivanov et al., 2015b). A nearly complete whorl of a young *Helicoprion* (KUPV 30606) was collected from GUMO in the Cutoff Formation (Chorn, 1978; GUMO staff pers. comm. to VLS, 2018).

Ivanov et al. (2012; 2021a) described the presence of a chondrichthyan assemblage from a quarry due east of the

southeast corner of GUMO representing the Williams Ranch Member of the Cutoff Formation. This assemblage included the symmoriiforms *Stethacanthulus decorus*, *Kunguroodus* sp., and an indeterminate form, the jalodontids *Adamantina foliacea* and *Isacrodus marthae*, the ctenacanth *Glikmanius myachkovensis*, an indeterminate hybodontiform, the sphenacanthid euselachian *Sphenacanthus* sp., the anachronistids *Cooleyella amazonensis*, *Cooleyella* sp., and *Reifella lata*, an indeterminate euchondrocephalan, and miscellaneous chondrichthyan denticles.

#### Mammoth Cave National Park, Kentucky (MACA)

The Mammoth Cave National Park in south-central Kentucky has one of the most diverse and extensive Late Mississippian chondrichthyan records (Fig. 5) in North America. More than one hundred and ten different species of chondrichthyans have been identified from four formations within the park, particularly within the extensive cave passageways. These beds represent the Viséan and Serpukhovian ages of the Middle and Late Mississippian. Much of the taxonomic work of the four chondrichthyan assemblages found within the park is still underway. Below is a summary of what has been identified so far.

#### Middle Mississippian

**St. Louis Formation**—The Horse Cave Member of the St. Louis Formation is the oldest of the limestone beds within MACA with chondrichthyan fossils and is Viséan in age. The St. Louis Formation is one of two geologic units in the park that preserve three-dimensional calcified cartilage from chondrichthyans. At present, twenty-three taxa of chondrichthyans have been identified from the Horse Cave Member based on isolated teeth collected within the cave. Five species of ctenacanthiform sharks are known: *Cladodus mirabilis*, *Cladodus elegans*, *Saivodus striatus*, *Glencartius costellatus*, and an indeterminate taxon. The St. Louis Formation is also notable for the occurrence of large ctenacanthiform dorsal fin spines, which presently are not found in any of the younger formations. The rest of the MACA chondrichthyan assemblage from the St. Louis Formation consist of members of the Euchondrocephali. At least two species of indeterminate paraselachians are known. The Orodontiformes is represented by *Leiodus calcaratus* and an indeterminate taxon. Petalodontiforms are represented by four taxa: *Chomatodus* sp., *Tanodus pumilis*, *Polyrhizodus concavus*, and *Petalorhynchus pseudosagittatus*. Holocephalans are known from ten taxa: *Helodus* sp., *Psephodus* sp., *Cochliodus* sp., *Deltodus* sp.,

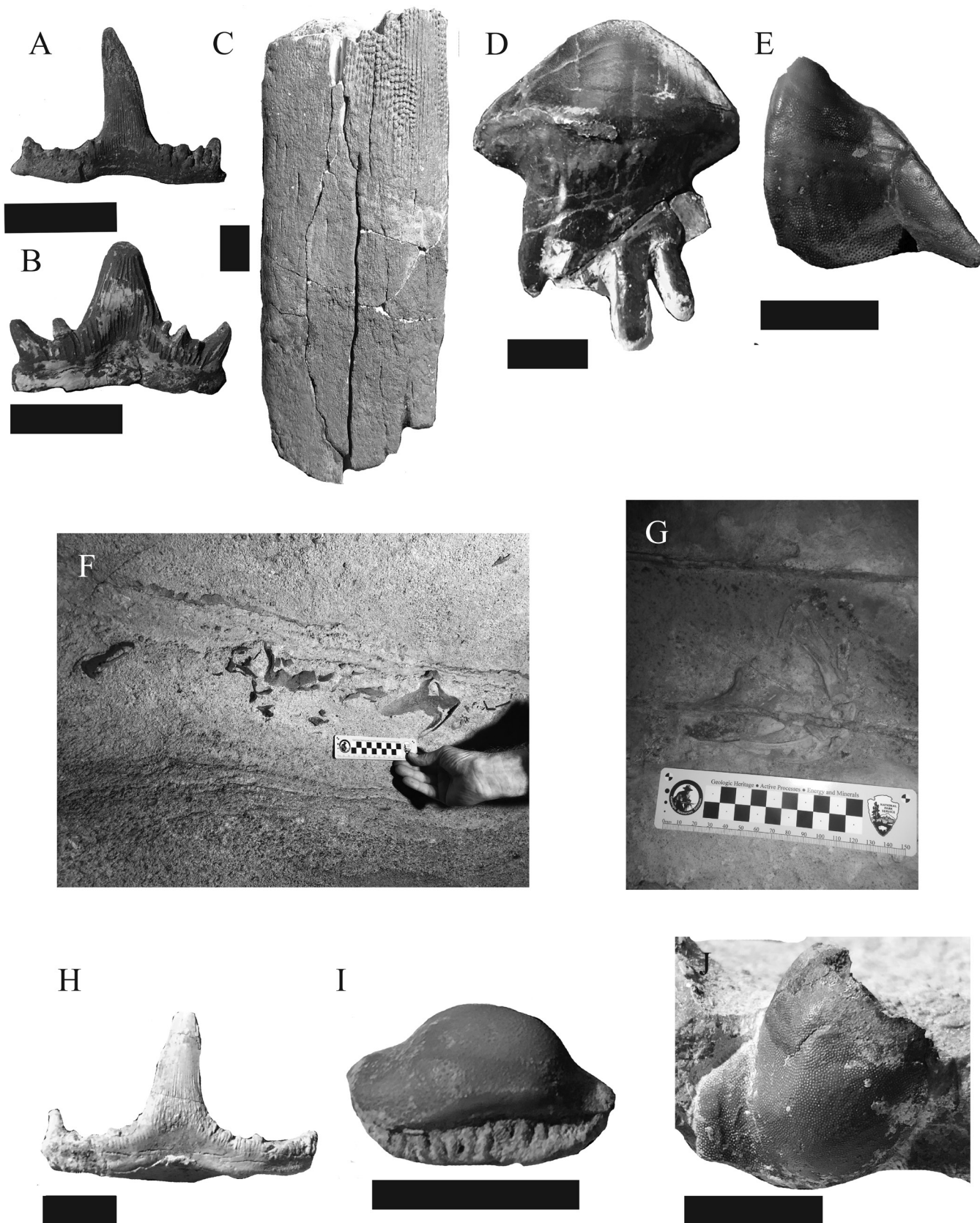


FIGURE 5. Sample of chondrichthyan fossils from Mammoth Cave National Park, Kentucky. A-E) Chondrichthyans from the Middle Mississippian St. Louis Formation. A) *Saivodus striatus*, B) *Cladodus mirabilis*, C) *Bythiacanthus* sp., D) *Polyrhizodus concavus*, E) *Deltoptychius* sp. F-G) Chondrichthyan skeletal material from the Middle Mississippian Ste. Genevieve. F) lower jaw and cranial cartilages of *Saivodus striatus*, G) the upper and lower jaws of *Glikmanius* sp. H-J) Chondrichthyans from the Late Mississippian Girkin Formation. H) *Saivodus striatus*, I) *Helodus* sp., J) *Cochliodus* sp. Scale equal 1 cm.

*Sandalodus* sp., *Poecilodus* sp., *Psammodus* sp., *Copodus cornutus*, *Deltoptychius* sp., and *Traquairus* sp.

The St. Louis Formation differs from the overlying Ste. Genevieve Formation in the presence of *Cladodus elegans*, *Tanodus pumilis*, *Polyrhizodus concavus*, and *Copodus cornutus*. The absence of these taxa in the Ste. Genevieve Formation may be in part either environmental preferences of these taxa not being met within the Ste. Genevieve environmental system or due to extinction.

**Ste. Genevieve Formation**—The Ste. Genevieve Formation has three geologic members with known chondrichthyan fossils, the Fredonia, the Karnack, and Joppa members. This formation and associated shark fauna are also Viséan in age. Of these three geologic units, the Joppa Member has the most diverse assemblage, with fifty-three species identified. Aside from the varying number of species in each member, all three members have the same common taxa. At least four symmoriiform chondrichthyans are currently known, two indeterminate species of *Stethacanthus* and two indeterminate species of *Denaea*. The phoebodonts *Thrinacodus* cf. *dziki* and an indeterminate species are present and were collected from screenwash samples. Two species of the marine xenacanth *Bransonella*, *B. nebraskensis* and *B. lingulata*, have been identified. At least seven ctenacanthiform sharks have been collected: *Cladodus mirabilis*, a new “*Cladodus*-like” taxon, *Saivodus striatus*, a new species of *Glikmanius*, *Glencartis costellatus*, and two indeterminate species. Both the *Cladodus mirabilis* and *Saivodus striatus* samples include individual teeth reaching 3 cm or more, representing large-bodied sharks approximately 4–5 meters or greater in length. At least three euselachian chondrichthyans have been collected from screenwashed sediments: an indeterminate protacrodontiform, an indeterminate hybodontiform, and cf. *Cooleyella* sp.

The Euchondrocephali of the Ste. Genevieve Formation are very diverse. At least six kinds of paraselachians, including *Heteropetalus* sp., *Venustodus* sp., *Euglossodus* sp., and four indeterminate forms are known. There are four taxa of Orodontiformes which include two species of *Orodus*, *Leiodus* sp., and an indeterminate species. There is one eugenodontiform present. Petalodonts are highly diverse with twelve species known: two species of *Chomatodus*, a new species of *Janassa*, *Petalodus hastingsii*, *Petalodus linguifer*, a new species of *Petalodus*, *Lisgodus* sp., *Petalorhynchus spatulatus*, a obruchevodid, cf. *Belantsea* sp., and two indeterminate species. The Holocephali are also very diverse with ten species known: a chondrenchelyid, *Helodus* sp., *Psephodus* sp., *Cochliodus* sp., *Deltodus* sp., *Sandalodus* sp., *Poecilodus* sp. cf. *Solenodus* sp., *Psammodus* sp., and *Deltoptychius* sp.

#### Late Mississippian

**Girkin Formation**—The Girkin Formation is Serpukhovian in age and at present only eleven species of chondrichthyans are recognized at MACA. These taxa include the ctenacanthiform *Saivodus striatus*, an indeterminate paraselachian, an indeterminate eugenodont, two species of petalodonts, *Petalorhynchus* cf. *P. beargulchensis*, and the holocephalans *Helodus* sp., *Psephodus* sp., *Cochliodus* sp.? *Deltodus* sp., and an indeterminate holocephalan.

**Haney Formation**—The Haney Formation is the last and youngest of the four formations in MACA with chondrichthyan fossils. This Serpukhovian-age formation has a few fossiliferous cave sites exposed within MACA. Presently, only four species are recognized in the Haney Formation at MACA; the ctenacanthiform ?*Glikmanius* sp., an indeterminate euchondrocephalan, the petalodont *Petalodus* sp., and the holocephalan *Psephodus* sp.

#### Natchez Trace Parkway, Alabama (NATR)

##### Middle Mississippian

**Tuscumbia Limestone**—A recent survey of a cave within Natchez Trace Parkway in Colbert County, Alabama by the lead author (JPH) has led to the identification of chondrichthyan fossils within the Middle Mississippian (Viséan) Tuscumbia Limestone (Fig. 6). Presently we have identified at least six taxa; an indeterminate cladodont (either symmoriiform or ctenacanthiform), the petalodontomorphs *Petalodus* sp., *Polyrhizodus* sp., and *Chomatodus* sp., and the holocephalan chondrichthyans *Helodus* sp. and *Deltodus* sp. The depositional environment of the Tuscumbia Limestone represents a warm shallow sea with rather clear waters (Lacefield, 2013).

#### Pecos National Historical Park, New Mexico (PECO)

##### Late Pennsylvanian to Early Permian

**Sangre de Cristo Formation**—A single chondrichthyan record is known from the Sangre de Cristo Formation in Pecos National Historical Park (Romer 1960). Romer (1960) noted the presence of isolated teeth of *Xenacanthus* occurring from multiple localities within this formation. Whether these teeth represent *Xenacanthus* or *Orthacanthus*, another common xenacanth from the Permian freshwater beds of the American southwest, is still to be determined and warrants further investigation.

#### Yellowstone National Park, Wyoming, Montana, and Idaho (YELL)

##### Mississippian

**Madison Group**—A single holocephalan tooth plate was reported from the Madison Limestone at Yellowstone National Park (YELL), in Wyoming (Santucci, 1998; Tweet et al., 2013). Recent examination of this specimen (YELL 133374, Fig. 4A) places this tooth within the holocephalan taxon *Helodus* cf. *H. didymus*, the same taxon found within the Middle Mississippian (Viséan) Redwall Limestone at GRCA (Hodnett et al., 2021). This would be the second record of this taxon outside of Ireland.

##### Permian

**Shedhorn Sandstone/Phosphoria Formation**—Yochelson and Van Sickle (1968) reported the teeth of the petalodont *Janassa* and the holocephalan *Helodus* from Shedhorn Sandstone beds near the southern border of YELL. Reports of the occurrence of the eugenodont *Helicoprion* from the Phosphoria Formation at YELL have been made (Hunt et al., 2006). This genus is well known in the Phosphoria Formation in the region of YELL (Bendix-Almgreen, 1966; Tapanila and Pruitt, 2013). However, the YELL record of *Helicoprion* has yet to be substantiated with a physical specimen.

#### MESOZOIC

During the Permian/Triassic extinction event (ending approximately 252 mya) a majority of the chondrichthyan orders common throughout much of the Paleozoic were lost due to extinction or greatly reduced in number. Orders such as Protacrodontiformes, Paraselachii, Orodontiformes, and Petalodontiformes went extinct, while Xenacanthiformes, Phoebodontiformes, and Eugenodontiformes held on into the mid to late Triassic. The ctenacanthiforms and symmoriiforms appear to have survived into the Cretaceous by adapting to deeper waters (Guinot et al., 2013; Feichtinger et al., 2020). However, although Euselachii and Holocephali lost family groups respectively during the Permian/Triassic extinction, these groups underwent a second evolutionary radiation during the Mesozoic (Stahl, 1999; Cappetta, 2012; Friedman and Sallan, 2012).

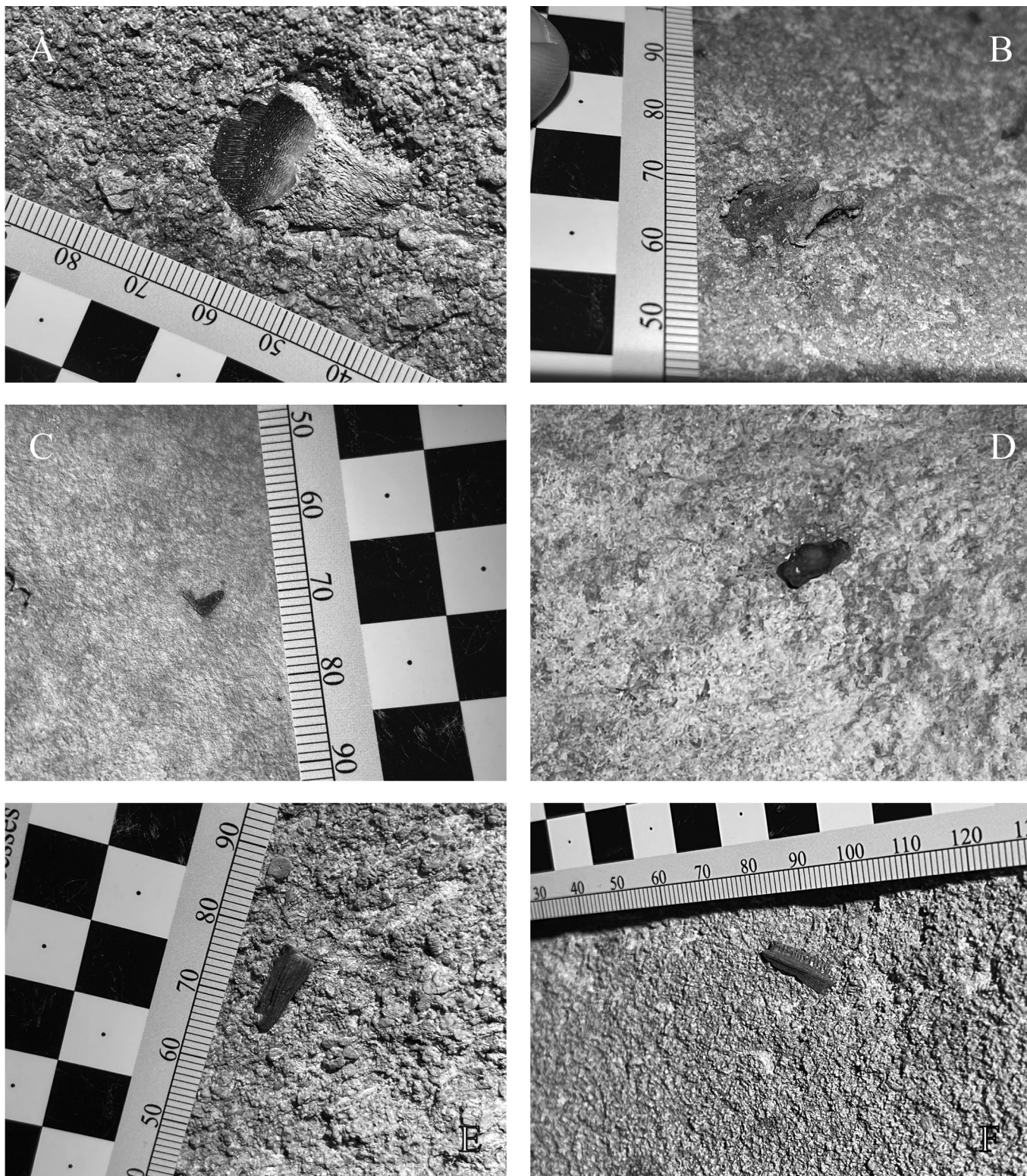


FIGURE 6. Chondrichthyan fossils from the Natchez Trace Parkway, Alabama. **A)** *Petalodus* sp., **B)** *Polyrhizodus* sp., **C)** indeterminate cladodont (ctenacanthiform or symmoriiform) grade tooth, **D)** *Helodus* sp., **E-F)** *Chomatodus* sp. Scale equal 1 cm.

The majority of the NPS units with Mesozoic chondrichthyan records are Cretaceous in age, which encompasses fifteen parks. The single exception is Petrified Forest National Park, which has a fairly diverse Late Triassic chondrichthyan assemblage. At present, no Jurassic records of chondrichthyans are known from NPS units. The Cretaceous records of chondrichthyans from NPS units include some of the last records of hybodont sharks, which went extinct by the end of the Late Cretaceous (Cappetta, 2012). The neoselachians went through a major radiation which saw the rise of the modern families of sharks and rays we see today. The most common neoselachian orders and families encountered at NPS units include (Fig. 7):

**Ptychodontidae**—An enigmatic family of extinct chondrichthyans that evolved dentition pavements of durophagous teeth (Cappetta, 2012; Hamm, 2020; Fig. 7B). At present, two genera, *Parapterygotus* and *Ptychodus*, are known from North America with the latter taxon including at least 16 species (Hamm, 2020). The ptychodont sharks first appeared during the Early Cretaceous (Aptian/Albian) and are known primarily from teeth, a few jaws, and some appendicular elements (Cappetta, 2012; Hamm, 2020). Presently, the relationships of the ptychodonts to other elasmobranch chondrichthyans are uncertain; they have been allied to the hybodonts and ctenacanthiforms, or considered their own distinct lineage (Cappetta, 2012).

**Orectolobiformes**—This order contains seven families which include the extant whale shark (*Rhincodon typus*), wobbegongs (genus *Eucrossorhinus* and *Orectolobus*), and bamboo sharks (genus *Chiloscyllium* and *Hemiscyllium*) (Cappetta, 2012; Fig. 7C). This order of sharks first appeared during the Jurassic.

**Lamniformes**—This order contains ten families, seven of which are still extant today, commonly called the mackerel sharks (Cappetta, 2012; Fig. 7A). This order includes the extant white shark (*Carcharodon carcharias*), the goblin shark (*Mitsukurina owstoni*) and the extinct massive Miocene shark, *Otodus megalodon* (Cappetta, 2012). Cretaceous sites within the NPS have a rich record of lamniform sharks.

**Batoidea**—This superorder of euselachian chondrichthyans include the extant electric rays (Torpediniformes) sawfish and guitarfish (Rhinopristiformes), skates (Rajiformes), and stingrays (Myliobatiformes), which are characterized by their ventral mouths and gill openings and enlarged pectoral fins (Cappetta, 2012; Fig. 7D). This superorder has its origins during the Jurassic.

### Badlands National Park, South Dakota (BADL)

#### Late Cretaceous

**Pierre Shale**—The Campanian Pierre Shale is a marine dark-gray shale deposited in the Western Interior Seaway. A tooth of the lamniform *Odontaspis* sp. (BADL 9935) is known from the Elk Butte Member of the Pierre Shale in BADL (Cicimurri et al., 1999).

**Fox Hills Formation**—The marginal marine Fox Hills Formation at BADL is of early Maastrichtian age and has a few undescribed shark fossils (Stoffer, 2003; Landman et al., 2013). A tooth of the lamniform *Odontaspis* sp. (BADL 9935) and a partial skeleton of an indeterminate chondrichthyan (BADL 20530) are in the park collections.

### Big Bend National Park, Texas (BIBE)

#### Late Cretaceous

**Boquillas Formation**—The Turonian Boquillas Formation is the oldest geologic unit at Big Bend National Park, Texas (BIBE) with chondrichthyan fossils, representing marine, platform carbonate beds. This unit is well-known for invertebrate fossils (Wick and Corrick, 2015). Vertebrate fossils are known from

the Boquillas Formation, such as mosasaurs and bony fish, but are uncommon (Wick, 2021). Maxwell et al. (1967) first noted the occurrence of shark teeth from the Boquillas Formation in BIBE but did not note the species. Wick and Corrick (2015) and Wick (2021) listed *Ptychodus mortoni* and an indeterminate form of chondrichthyan as occurring in the Boquillas Formation in BIBE.

**Pen Formation**—The Pen Formation represents shallow marine shelf mudstones of the early to mid-Campanian. Shark fossils are well represented in the Pen Formation with the following taxa: the orectolobiform *Cretoectolobus olsoni*, the lamniform sharks *Squalicorax kaupi* and *Cretoalamna appendiculata*, the batoid sawfish *Ischyrrhiza mira*, and the skate *Ptychotrygon* sp. (Lehman, 1985; Standhardt, 1986, 1989).

**Aguja Formation**—The Aguja Formation represents a continuing marine transgression, intertongued with nearshore terrestrial deposits of late Campanian to early Maastrichtian age (Fig. 8). Sharks are very diverse in the Aguja Formation at BIBE because they include both coastal marine forms and estuary and fluvial adapted species (Wick and Corrick, 2015; Wick, 2021). Taxa identified from the Aguja Formation of BIBE are: the hybodonts *Hybodus* sp. (though most likely *Meristodon montanensis*, vide Cappetta, 2012) and *Lissodus/Lonchidion selachos*; the orectolobiforms *Cretoectolobus olsoni* and *Squatirhina americana*; the lamniform sharks *Anomotodon augustidens*, *Scapanorhynchus raphiodon*, *Scapanorhynchus texanus*, *Cretoalamna appendiculata*, *Lamna* cf. *L. elegans*, and *Odontaspis* sp.; and the batoids *Ischyrrhiza avoncola*, *Ischyrrhiza mira*, *Onchopristis dunklei*, *Onchopristis* sp., *Ptychotrygon agujaensis*, and an indeterminate dasyatid stingray (Maxwell et al., 1967; Applegate, 1972; Davies, 1983; Lehman, 1985; Standhardt 1986, 1989; Sankey 1998, 2010). Schubert et al. (2016) recently reviewed the chondrichthyan assemblage of the Rattlesnake Mountain sandstone member of the Aguja Formation, adding the taxa *Cantioscyllium* aff. *C. meyeri*, *Chiloscyllium* aff. *C. greeni*, *Columbusia* sp., *Serratolamna* cf. *S. carabae*, *Squalicorax kaupi*, *Squalicorax* aff. *S. yangaensis*, *Squalicorax* aff. *S. lindstromi*, “*Rhinobatos*” sp., *Protoplatyrhina renae*, *Ptychotrygon triangularis*, *Texatrygon* cf. *T. copei*, *Rhombodus levis*, *Brachyrhizodus wichitaensis*, and *Igdabatis* cf. *I. indicus*.

### Bryce Canyon National Park (BRCA)

#### Late Cretaceous

**Straight Cliffs Formation**—The Smoky Hollow Member of the Straight Cliffs Formation has a some indeterminate sharks and rays from a regressive sequence that began during the deposition of the upper part of the underlying Tippet Canyon Member (Pearce, 2009; Tweet et al., 2012). Williamson et al. (2011) reported the occurrence of the myliobatid ray *Brachyrhizodus* sp. from the John Henry Member of the Straight Cliffs Formation at BRCA.

**Wahweap Formation**—BRCA has a number of localities in the Late Cretaceous (Campanian) Wahweap Formation that have produced vertebrate fossils, including the teeth of sharks and rays (Munk, 1998; Eaton, 1999). Kirkland et al. (2013) identified the batoid taxa *Columbusia delieuxi*, *Texatrygon brycensis*, *Cristomylus cifellii*, and the carpet shark *Chiloscyllium missouriense* from the Wahweap Formation at BRCA.

### Cabrillo National Monument, California (CABR)

#### Late Cretaceous

**Cabrillo Formation**—A single lamniform shark taxon, *Squalicorax* sp., has been identified from the Maastrichtian Cabrillo Formation of the Rosario Group of CABR (Koch and Santucci, 2003).

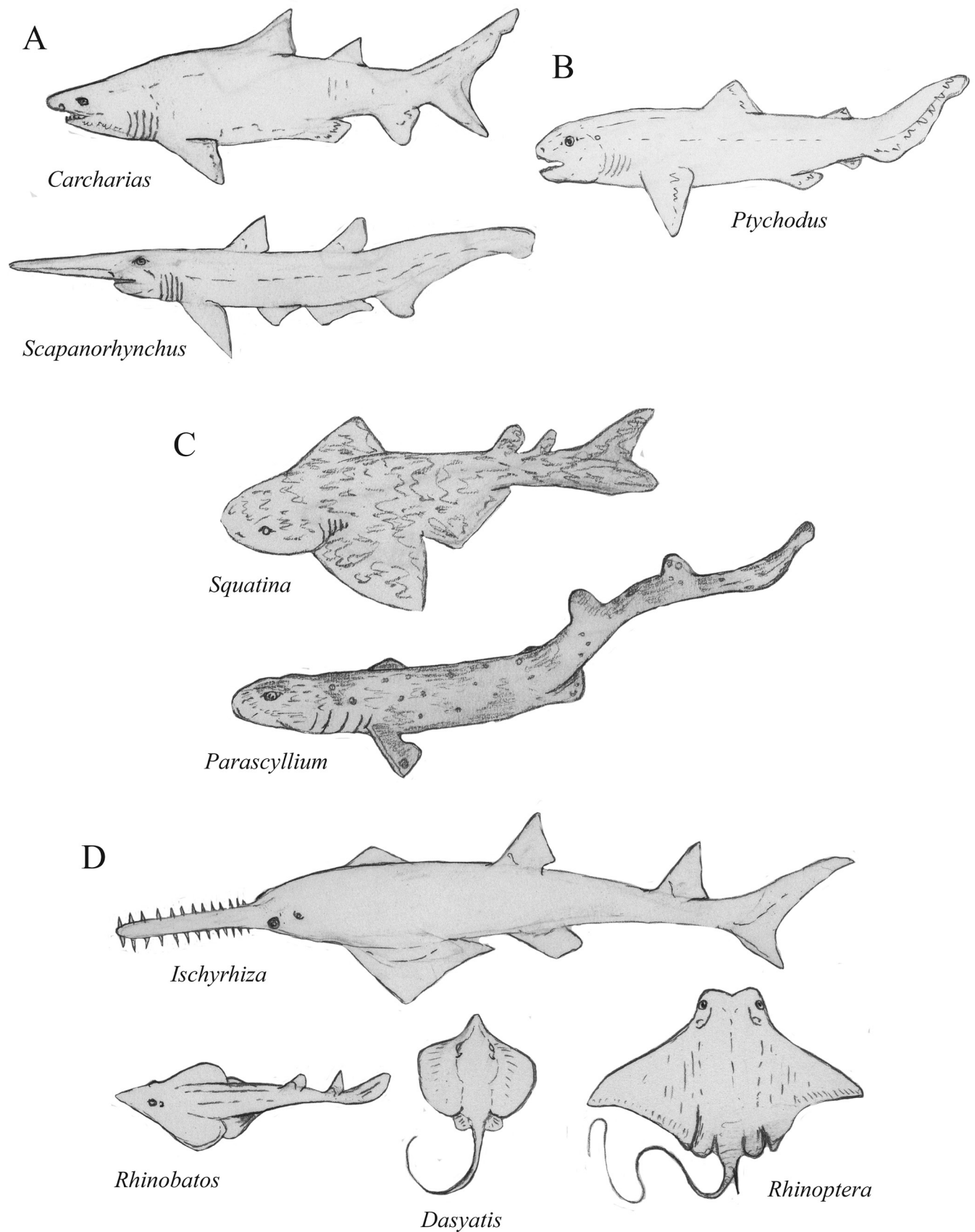


FIGURE 7. Representatives of Mesozoic and Cenozoic chondrichthyans from National Park Service units. A) Lamniformes with *Carcharias* and *Scapanorhynchus*. B) Ptychodontidae with *Ptychodus*. C) Squatiniformes and Orectolobiformes with *Squatina* and *Parascyllium*. D) Batoidea with *Ischyrrhiza*, *Rhinobatos*, *Dasyatis*, and *Rhinoptera*. Chondrichthyans not draw to scale between groups.

### Capitol Reef National Park, Utah (CARE)

#### Late Cretaceous

*Mancos Shale*—The Cenomanian to early Campanian marine Mancos Shale is exposed at Capitol Reef National Park, Utah (CARE). Presently, shark teeth have been reported to occur within the Mancos Shale at CARE, but no identifications have been presented at this time (Hunt et al., 2006).

### Chaco Culture National Historical Park, New Mexico (CHCU)

#### Late Cretaceous

*Cliff House Sandstone*—The middle Campanian Cliff House Sandstone represents a marine regression of the great interior seaway and is well exposed within Chaco Culture National Historical Park, New Mexico (CHCU) (Varela et al., 2019). Shark teeth have been encountered within the Cliff House Sandstone at CHCU, with the majority of them representing lamniform sharks. The taxa currently identified from within this unit are: *Squalicorax kaupi*, *Squalicorax pristodontus*, *Scapanorhynchus texanus*, cf. *Serratolamna* sp., *Archaeolamna kopingensis*, and a number of indeterminate lamniforms (Varela et al., 2019). This shark assemblage is awaiting formal description.

### Congaree National Park, South Carolina (CONG)

#### Late Cretaceous

*Undifferentiated Upper Cretaceous Rocks*—Tweet et al. (2009) reported the discovery of shark teeth from Congaree National Park, South Carolina (CONG) from drilling operations within the park in the 1980s.



FIGURE 8. Two isolated teeth of *Scapanorhynchus texanus* from the Rattlesnake Mountain Sandstone unit of the Late Cretaceous Aguja Formation at Big Bend National Park (BIBE), Texas. Scale equals 1 cm.

### Dinosaur National Monument, Colorado and Utah (DINO)

#### Early Cretaceous

*Mowry Shale*—Shark teeth have been reported from the Mowry Shale at Dinosaur National Monument. They pertain to the lamniform *Haimirchia amonensis* (Hansen et al., 1983; Scott et al., 2001; Anderson and Kowallis, 2005).

### Fort Washington Park, Maryland (FOWA)

#### Late Cretaceous

*Severn Formation*—The Severn Formation is well exposed in the Fort Washington Park region, representing a Maastrichtian marine shallow-water inner shelf (Kenworthy and Santucci, 2004). Late Cretaceous chondrichthyans are known from nearby sites and include the hybodont *Hybodus* sp. (most likely *Meristodon montanensis*; vide Cappetta, 2012), the selachians *Cretolamna* cf. *C. serreta*, *Cretolamna appendiculata*, *Squalicorax kaupi*, *Squalicorax pristodontus*, *Odontaspis* sp., *Hypotodus* sp., *Nebrius* sp., *Squatina hassei*, and the batoids *Ischyrrhiza mira*, and *Myliobatis* sp. (Hartstein and Decina, 1986; Hartstein et al., 1999). Erroneous records of *Isurus* sp. and *Hemipristis serra* have been listed as coming from the Severn Formation near Fort Washington Park at Piscataway Creek (Kenworthy and Santucci, 2004; and Hunt et al., 2006); however, both taxa are known only from the Miocene beds of the St. Mary's, Choptank, and Calvert Formations (Kent, 1994; see NACE discussion below).

### Glen Canyon National Recreation Area, Arizona and Utah (GLCA)

#### Late Cretaceous

*Tropic Shale*—The early Late Cretaceous (Cenomanian–Turonian) Tropic Shale exposed within the borders of Glen Canyon National Recreation Area and Grand Staircase-Escalante National Monument (Bureau of Land Management) represents a shallow marine deposition of the southern great interior seaway (Albright et al., 2013). A number of Tropic Shale shark teeth have been identified and collected within GLCA and just on the other side of the border of GLCA (in Grand Staircase-Escalante National Monument), including specimens of: the lamniforms *Scapanorhynchus raphiodon*, *Squalicorax curvatus*, *Cretoxyrhina mantelli*, *Cretolamna appendiculata*, a diverse record of the enigmatic euselachian family Ptychodontidae (*Ptychodus decurrens*, *Ptychodus* cf. *P. mammillaris*, *Ptychodus whipplei*, *Ptychodus occidentalis*, *Ptychodus anonymous*, and *Ptychodus* sp.) and the batoid cf. *Ptychotrygon* sp. (Peterson, 1969; Albright et al., 2013).

*Straight Cliffs Formation*—The mid Late Cretaceous (Turonian-early Campanian) Straight Cliffs Formation contains fluvial, paralic, and marginal marine sediments. Peterson (1969) listed the occurrence of *Ptychodus* sp. in the John Henry Member of the Straight Cliffs Formation at GLCA.

### Mesa Verde National Park, Colorado (MEVE)

#### Late Cretaceous

*Cliff House Sandstone*—Harrison et al. (2017) noted the occurrence of teeth of the lamniform *Scapanorhynchus* sp. and the batoid *Ischyrrhiza* sp., as well as a number of indeterminate shark teeth and a possible shark vertebra from Mesa Verde National Park. Two specimens of fossil holocephalan egg cases have been documented from the Cliff House Sandstone at MEVE that are assigned to the ichnotaxon *Chimaerotheca gilli*, marking the evidence of holocephalans occurring in this formation (Harrison et al., 2021).

*Mancos Shale*—Leckie et al. (1997) and Harrison et al. (2017) noted a group of shark teeth in the MEVE park collections from the Mancos Shale just outside of the park boundary. The

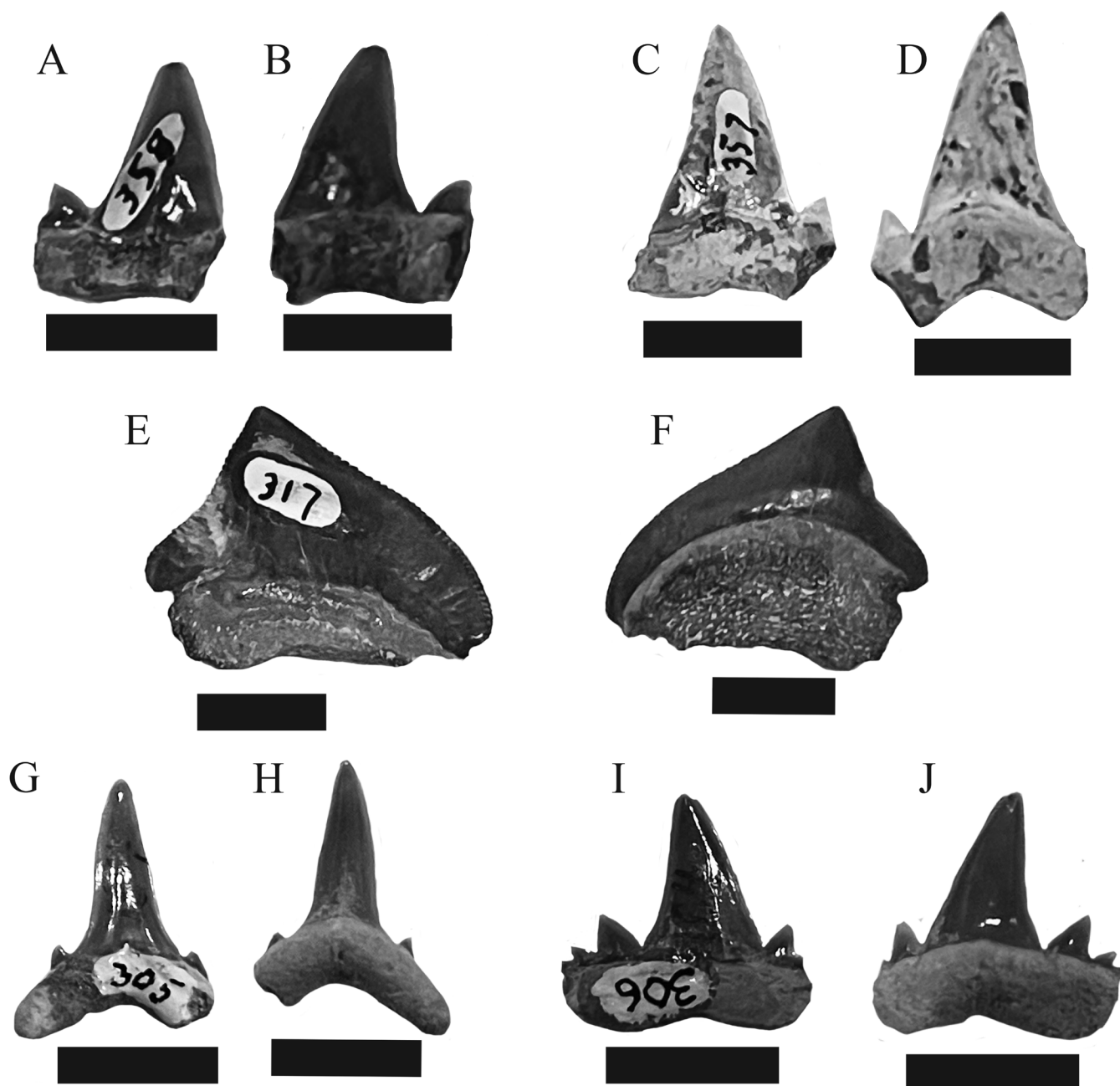


FIGURE 9. Chondrichthyan fossils from the Late Cretaceous (Maastrichtian) Prairie Bluff Chalk, at Natchez Trace Parkway, Mississippi. **A-D)** *Odontaspis cuspidate*; **A-B)** NATR 358, **A)** labial view, **B)** lingual view; **C-D)** NATR 357, **C)** labial view, **D)** lingual view. **E-F)** NATR 317, *Squalicorax pristodontus*, **E)** labial view, **F)** lingual view. **G-H)** NATR 305, *Striatolamia elegans*; **G)** labial view, **H)** lingual view. **I-J)** NATR 306, *Serratolamna* sp.; **I)** labial view, **J)** lingual view. Scale equal 1 cm.

collection contains the teeth of *Cretoxyrhina* sp., *Lamna* sp., *Plicolamna semiplicata*, *Ptychodus anonymous*, *Ptychodus decurrens*, *Ptychodus whipplei*, and *Squalicorax falcatus* (Harrison et al., 2017).

#### Missouri National Recreational River (MNRR)

##### Late Cretaceous

*Niobrara Formation*—Maher et al. (2003) reported shark teeth from the Niobrara Formation within Niobrara State Park. MNRR's boundaries partially overlap Niobrara State Park. The Niobrara Formation is the lowest formation present at the state park and is exposed in the lower parts of the Missouri and Niobrara River valleys. This is an area coincident with the

majority of the MNRR overlap, so there is a very good chance that the Niobrara Formation shark teeth of the state park were found in an area that overlaps the boundaries of MNRR.

*Carlisle Shale*—Johnson-Ransom et al. (2016) reported on a tooth of *Cretoxyrhina mantelli* from the Fairport Chalky Shale Member of the Carlisle Shale at MNRR.

#### Natchez Trace Parkway, Mississippi (NATR)

##### Late Cretaceous

*Prairie Bluff Chalk*—The Late Cretaceous (Maastrichtian) Prairie Bluff Chalk is well known for a rich marine invertebrate fauna that includes multiple species of gastropods, bivalves, nautiloids, ammonoids, and crinoids (Dockery and Thompson,

2016). A locality on the Natchez Trace Parkway in northeastern Mississippi produced a small number of shark teeth collected by NATR naturalist D. M. Black in the early 1960s. These teeth included examples of the lamniforms *Squalicorax pristodontus*, *Serratolamna* sp., *Araloselachus cuspidata*, and *Striatolamia elegans* (Fig. 9).

### Petrified Forest National Park, Arizona (PEFO)

#### Late Triassic

*Chinle Formation*—The Late Triassic Chinle Formation at Petrified Forest National Park in northeastern Arizona has a diverse record of flora and fauna (Irmis, 2005). This formation represents a large fluvial system that drained towards the western coast of Pangea (Sadler et al., 2015). This drainage has produced four distinct members with chondrichthyan fossils at and near PEFO, from oldest to youngest: the Blue Mesa Member, a tropical meandering river and swamp system; the Sonsela Member, a braided, sandy, river system representing the beginning of arid conditions with seasonal rains; the Petrified Forest Member, which was an even more arid river system with seasonal rains; and the youngest Owl Rock Member, representing lakes and some rivers amongst sand dunes (Sadler et al., 2015).

The Chinle Formation at PEFO has one of the last occurrences of the dominantly Paleozoic order of basal chondrichthyans, the Xenacanthiformes (Figs. 10A-B). The freshwater xenacanth *Mooreodontus moorei* is known primarily from the lower Blue Mesa Member of the Chinle Formation at PEFO and other Blue Mesa localities outside of the park (such as the *Placierias* or Downs quarries near St. Johns, Arizona) but is also known from the Tecovas Formation of the Dockum Group in Texas (Jacobs and Murry, 1980; Johnson, 1980; Kaye and Padian, 1994; Parker, 2005; Heckert et al., 2005). This xenacanth taxon was previously placed in the Carboniferous–Permian genus *Xenacanthus* but has been reclassified into its own genus (Ginter et al., 2010; Cappetta, 2012). Another basal chondrichthyan referred to as “*Phoebodus* sp.” was first reported from the Blue Mesa Member *Placierias* Quarry by Kaye and Padian (1994) based on a small unique non-xenacanth tricuspid tooth. Similar teeth have recently been collected from two Blue Mesa Member sites within PEFO (Ben Kligman and Adam Marsh, pers. commun., 2021). *Phoebodus* has tricuspid to seven-cuspid teeth and is known primarily from Middle to Late Devonian localities. However, *Phoebodus brodiei* was recently reported from Late Triassic sites in England and Germany (Cappetta, 2012; Ivanov et al., 2021a). Ivanov et al. (2021b) have reclassified these Late Triassic *Phoebodus*-like tricuspid teeth as belonging to a new genus of jalodontid chondrichthyan, *Keuperodus brodiei*. Jalodontids are a group of basal chondrichthyans with an extensive fossil record from the Devonian to the Late Triassic (Ivanov et al., 2021b). If the PEFO and *Placierias* Quarry *Phoebodus*-like teeth are examples of *Keuperodus*, they would be the first record of this taxon in North America.

The Chinle Formation also has a diverse hybodontiform record with at least two genera identified from PEFO (Figs. 10C-F). The hybodont family Lonchididae is represented in the Chinle Formation by the taxon *Lonchidion humblei*, which is also known from the Dockum Group in Texas (Murray, 1981). At PEFO, *Lonchidion humblei* is known primarily from the Blue Mesa Member (Jacobs and Murry, 1980; Murry and Kirby, 2002; Heckert, 2004; Irmis, 2005; Parker, 2005). Teeth of *Acrodus* sp., a member of the durophagous hybodont family Acrodontidae, have also been reported from the Blue Mesa Member at PEFO (Parker, 2005; Cappetta, 2012). Heckert (2004) also reported a number of indeterminate hybodont dermal denticles and fragmentary dorsal fin spines from the “Dying Grounds” site in the Blue Mesa Member of PEFO. The freshwater hybodont taxon *Reticulodus synergus* is abundant throughout the upper Chinle Beds at PEFO (Murry and Kirby, 2002; Voris and

Heckert, 2017). Isolated teeth of adult and juvenile *Reticulodus* have been found in the Sonsela and Petrified Forest members within PEFO, and have been found in the Owl Rock Member outside of the park. Taxonomically, *Reticulodus* has been placed in either the family Hybodontidae (Murry and Kirby, 2002; Voris and Heckert, 2017) or in the family Distobatidae (Cappetta, 2012). At present it seems *Reticulodus* is the only chondrichthyan taxon known above the Blue Mesa Member in the Chinle Formation (Murry and Kirby, 2002; Parker, 2005; Voris and Heckert, 2017). Fischer et al. (2010) reported on a new form of hybodont egg capsules from PEFO, *Palaeoxyris humblei*, which they interpreted as possibly associated with *Lonchidion humblei*.

### Santa Fe National Historic Trail, New Mexico (SAFE)

#### Late Cretaceous

*Carlile Shale*—In 1859, John Strong Newberry was participating in the Macomb expedition and stopped at the “Breaks of the Red River” [Canadian River] southeast of Springer, New Mexico on the Santa Fe Trail. While there, he documented a stratigraphic section. In his unit 3, a ferruginous laminated sandy limestone (attributed by Hook and Cobban, 1980 to the Juana Lopez and Blue Hill Members of the Carlile Shale), he observed shark teeth (*Lamna* and *Oxyrhina*) (Newberry, 1876). We include this record because it is tied to the history of the national historic trail.

### Yellowstone National Park, Wyoming, Montana, and Idaho (YELL)

#### Early Cretaceous

*Mowry Shale*—The Mowry Shale is an Early Cretaceous dark shale unit exposed in the northern part of Yellowstone National Park. The Mowry Shale was deposited along the western margins of the Cretaceous Interior Seaway and is considered to date to the late Albian age (Ludvigson et al., 2010). The Mowry Shale is known for the abundance of fish fossils, primarily isolated scales, teeth, and bones that were deposited during storm activity (Cockerell, 1919; Anderson and Kowallis, 2005; Steward and Hakel, 2006). Though most of these fish remains are disarticulated and disassociated, there are a few records of articulated fish occurring in the Mowry Shale (Dunkle, 1971).

The YELL Mowry Shale fish assemblage is presently undescribed and was mostly known from isolated scales and teeth collected in 2001. Recently, one of the coauthors (VLS) collected a shark dorsal fin spine during a preliminary survey of a YELL Mowry Shale site in 2021. The spine is overall narrow, approximately 36 mm long, and approximately 3 mm wide near the base. Though fragmentary, longitudinal smooth costae can be seen. No indication of posterior-facing denticles near the tip of the spine can be seen, though this could be due to the orientation of the spine in the rock. We tentatively refer this spine to a hybodontiform chondrichthyan. Outside of the YELL Mowry Shale assemblage, the neoselachian *Haimirichia amonensis* is known from the Mowry Shale near Vernal, Utah (Anderson and Kowallis, 2005).

#### Late Cretaceous

*Frontier Formation*—A single tooth of an indeterminate shark is noted by Tysdal et al. (1990) from the Cenomanian–Turonian Frontier Formation exposed at Mount Everts in the northwest part of YELL. At this time, this shark tooth has not been located in any museum collection.

## CENOZOIC

The Cenozoic represents the time interval where all modern families of sharks and rays were present on the planet, and many modern genera of sharks and rays first evolved early in the Cenozoic (Cappetta, 2012). The hybodonts, which flourished in

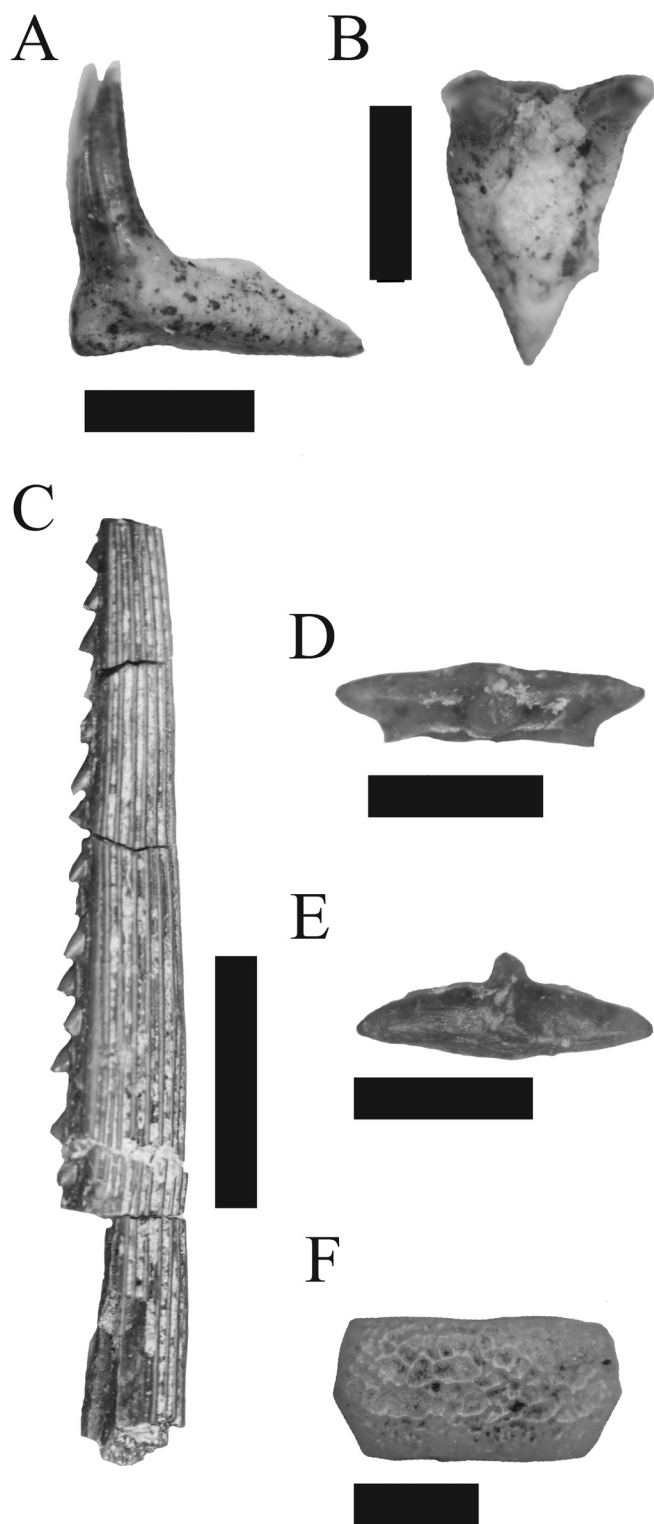


FIGURE 10. Chondrichthyan fossils from the Late Triassic Chinle Formation, at Petrified Forest National Park, Arizona. **A-B)** PEFO 49158, the Triassic xenacanthid *Mooreodontus moorei*, anterolateral tooth in **A)** mesial, **B)** oral. **C-F)** Hybodontiform fossils. **C)** PEFO 46582, hybodontiform indeterminate dorsal fin spine in right lateral view. **D-E)** PEFO 48775, *Lonchidion humblei*, lateral tooth in **D)** labial, **E)** oral. **F)** PEFO 3831B, *Reticulodus synergus*, lateral tooth in oral view. Scale A-B, D-E, and F equal 2 mm; C equals 1 cm.

the late Paleozoic and Mesozoic, went extinct at the end of the Cretaceous Period. Some shark families, such as Otodontidae, which first appeared during the Cretaceous, reached great lengths, with their peak size seen in *Otodus megalodon* which approached close to 20 meters in length or greater (Perez et al., 2021). However, by the Pliocene, these large sharks went extinct (Boessebecker, et al., 2019).

The majority of the NPS units with Cenozoic chondrichthyan fossils typically are located near the coastal regions of the United States. Some exceptions, such as Big Bend National Park, Texas and Fossil Butte National Monument, Wyoming, represent older deposits that either were closer to the ancient shoreline or represent large freshwater lakes with chondrichthyans adapted to those environments. Cenozoic chondrichthyans, from the Paleocene (Texas and Maryland) to Pleistocene/Holocene (Georgia), are recognized from seventeen NPS units.

#### Big Bend National Park, Texas (BIBE)

##### Paleocene

*Black Peaks Formation*—The upper Black Peaks Formation represents the Paleocene (Puercan–Tiffanian) and is noted for garfish, turtles and mammals (Wick, 2021). Teeth of two taxa of stingrays referred to *Rhombodus* sp. and *Dasyatis* sp. were identified from BIBE localities by Standhardt (1986). *Rhombodus* is of particular interest as it known primarily from Late Cretaceous (Campanian–Maastrichtian) sites around the world, though there is also a tentative lower Paleocene record from the Littig Formation in Texas (Cappetta, 2012).

##### Eocene

*Hannold Hill Formation*—The Hannold Hill Formation represents a fluvial sandstone channel deposition and is known for large Eocene mammals (Wick, 2021). Standhardt (1989) listed the occurrence of the eagle ray *Myliobatis* sp. within the Hannold Hill Formation. The occurrence of *Myliobatis* within the fluvial system of the Hannold Hill Formation is of interest, as extant eagle rays occur in shallow marine coastal waters and are not known to travel up rivers.

#### Channel Islands National Park, California (CHIS)

##### Miocene–Quaternary

Channel Islands National Park consists of five islands (Anacapa, Santa Barbara, Santa Cruz, San Miguel, and Santa Rosa) which are part of eight islands off the southern California coast. Fossils of chondrichthyans, primarily isolated teeth of unidentified sharks and rays, are known from the Miocene to Pleistocene on many of these islands (Tweet et al., 2020). Late Oligocene–Miocene ray and shark teeth are known from the Vaqueros Formation of Santa Cruz and Santa Rosa Islands (Tweet et al., 2020). Early Miocene shark and ray teeth are known from the Rincon Formation on Santa Rosa Island (Tweet et al., 2020). The angel shark *Squatina californica*, an indeterminate leopard shark (Family Triakidae), and other indeterminate elasmobranch fossils are known from Quaternary sediments on San Miguel Island (Tweet et al., 2020).

#### Colonial National Historical Park, Virginia (COLO)

##### Pliocene

*Yorktown Formation*—A number of Pliocene shark teeth have been recorded from the marine Yorktown Formation at Colonial National Historical Park (Johnson, 1972; Burns, 1991). These shark teeth from COLO include the large lamniform shark *Carcharodon hastalis*, the sand tiger shark *Eugomphodus* (*Carcharias*) sp., the extinct seven-gill cow shark *Notorhynchus primigenius*, the tiger shark *Galeocerdo aduncus*, the gray shark *Carcharhinus egertoni*, and a number of indeterminate ray teeth and dermal elements (Burns, 1991).

### Cumberland Island National Seashore, Georgia (CUIS)

#### Miocene–Holocene

*Mixed and unnamed formations*—Teeth of indeterminate shark and rays have been collected from dredge spoil piles near the south end of Cumberland Island National Seashore, Georgia (Tweet et al., 2009). The dredge spoils came from the Cumberland River and Sound during the construction of nearby military installations (Tweet et al., 2009).

### El Camino Real de los Tejas National Historic Trail, Texas (ELTE)

#### Middle Eocene

*Crockett Formation*—Stenzel et al. (1957) listed the occurrence of isolated indeterminate shark and ray teeth in the Middle Eocene Stone City Member of the Crockett Formation along the route of the historic trail at the Stone City Bluff crossing, near Bryan–College Station and nearly due east of Austin, Texas.

### Everglades National Park, Florida (EVER)

#### Late Cenozoic

*Hawthorn Group*—Parker and Cooke (1944) mentioned the presence of shark teeth in a core taken from Everglades National Park. The teeth came from an indeterminate geologic horizon within the Late Cenozoic Hawthorn Group.

### Fort Matanzas National Monument, Florida (FOMA)

#### Upper Pleistocene

*Anastasia Formation*—Teeth of unidentified sharks and rays are known from the Anastasia Formation at Fort Matanzas National Monument, Florida, which consists of a Pleistocene sandy coquina exposed along the beach (Tweet et al., 2009).

### Fort Monroe National Monument, Virginia (FOMR)

#### Oligocene–middle Miocene

?*Calvert Formation*—Shark teeth were discovered in 1864 during the construction of a well at Fort Monroe, at a depth of approximately 177–180 meters (Rogers, 1882; Tweet et al., 2014).

### Fort Pulaski National Monument, Georgia (FOPU)

#### Lower Miocene

*Marks Head Formation*—Pratt and Petkewich (1989) briefly mentioned the occurrence of at least 11 species of sharks and rays from the Marks Head Formation (Hemingfordian) in close proximity to Fort Pulaski National Monument, Georgia (FOPU).

#### Late Miocene

*Ebenezer Formation*—Weems and Edwards (2001) reported on the teeth of the sharks *Negaprion eurybathrodon* and *Rhizoprionodon* sp. and indeterminate myliobatid ray tooth fragments from FOPU in the Ebenezer Formation.

#### Pleistocene–Holocene

*Quaternary Deposits*—Shark and ray teeth are known from Pleistocene sediments in close proximity to FOPU (Tweet et al., 2009).

### Fossil Butte National Monument, Wyoming (FOBU)

#### Eocene

*Green River Formation*—The fossil record documented at Fossil Butte National Monument in Wyoming is a world-renowned Lagerstätten with an extraordinary abundance, diversity and preservation of fossils found in the lacustrine sediments of ancient Fossil Lake. Among the fossils is a large

diversity of fishes. Two extinct freshwater stingray taxa are known from complete adults to neonatal juveniles, the earliest described *Heliobatis radians* (Marsh, 1877) and the recently described *Asterotrygon maloneyi* (De Carvalho et al., 2004).

### George Washington Birthplace National Monument, Virginia (GEWA)

#### Miocene

*Calvert Formation*—Teeth of *Otodus obliquus* (most likely *O. megalodon*; V. Perez pers comm, 2022), *Hemipristis serra*, and *Isurus desorii* have been reported from George Washington Birthplace National Monument, Virginia (GEWA), as well as teeth of *Isurus* (mako), *Carcharius* (sand tiger), *Carcharhinus* (silky), and *Carcharodon* (white sharks) (McLennan, 1971; Hunt et al., 2006). Excavations of marine mammal fossils from GEWA also yielded *Physogaleus contortus*, *Carcharodon* sp., and *Hemipristis* sp. (Kenworthy and Santucci, 2003). The Calvert Formation has a rich assemblage of chondrichthyans (54 species; 3 holocephalans, 39 sharks and 18 ray species) throughout the mid-Atlantic region (Kent, 2018).

### Gulf Islands National Seashore, Florida and Mississippi (GUIS)

#### Cenozoic

*Multiple coastal deposits*—A recent Paleontological Resource Inventory of the Gulf Islands National Seashore has documented a number of new shark taxa. In the Florida portion of GUIS, fossil chondrichthyans were documented which appear to be potentially reworked from the Oligocene Chickasawhay Limestone, the Pliocene Perdido Key and Citronelle formations, and the Pleistocene Biloxi and Gulfport formations (M. Clinton and C. Visaggi, written comm., 2021). Identified taxa from this survey include teeth of the sharks *Carcharinus*, *Galeocerdo*, *Rhizoprionodon*, and *Sphyrna*, indeterminate myliobatiform ray teeth, and holocephalan fin spines (M. Clinton and C. Visaggi, written comm., 2021).

### National Capital Parks East, Maryland (Fort Washington Park, Piscataway Park, and Suitland Parkway) (NACE)

#### Paleocene

*Brightseat Formation*—Lower Paleocene shark teeth are known from the Brightseat Formation in the vicinity of Suitland Parkway, Maryland (SUIT) (Nelson et al., 2019).

*Aquia Formation*—Teeth of the lamniform *Odontapsis* sp. and “*Isurus*” sp. and the myliobatiform *Rhinoptera* sp. have been reported from Fort Washington Park (FOWA) and Piscataway Park (PISC) (Kenworthy and Santucci, 2004 and 2006; Nelson et al., 2019; Fig. 11). The teeth of *Odontapsis* sp. are reidentified here as *Striatolamia* sp. (Fig. 11A–G). The “*Isurus*” sp. tooth has been diagnosed as a different genus and deriving possibly from the Calvert Formation (see below).

#### Miocene

*Calvert Formation*—Shark and ray teeth are known from the Calvert Formation in the vicinity of SUIT, including teeth of *Hemipristis serra* and *Carcharodon hastalis* that were collected in association with a baleen whale skeleton (Kenworthy and Santucci, 2004; Nelson et al., 2019; Fig. 12). An “*Isurus*” sp. tooth from FOWA, identified here as *Carcharodon* cf. *C. hastalis* (Fig. 12A–B) was originally referred to have derived from the Aquia Formation. However, *Carcharodon* is a taxon known only from the Miocene (Cappetta, 2012). The Calvert Formation is found at relatively high elevations in the FOWA area and could be the source of this specimen. Two additional indeterminate carcharinid teeth were also collected from FOWA and may have also derived from the Calvert Formation.

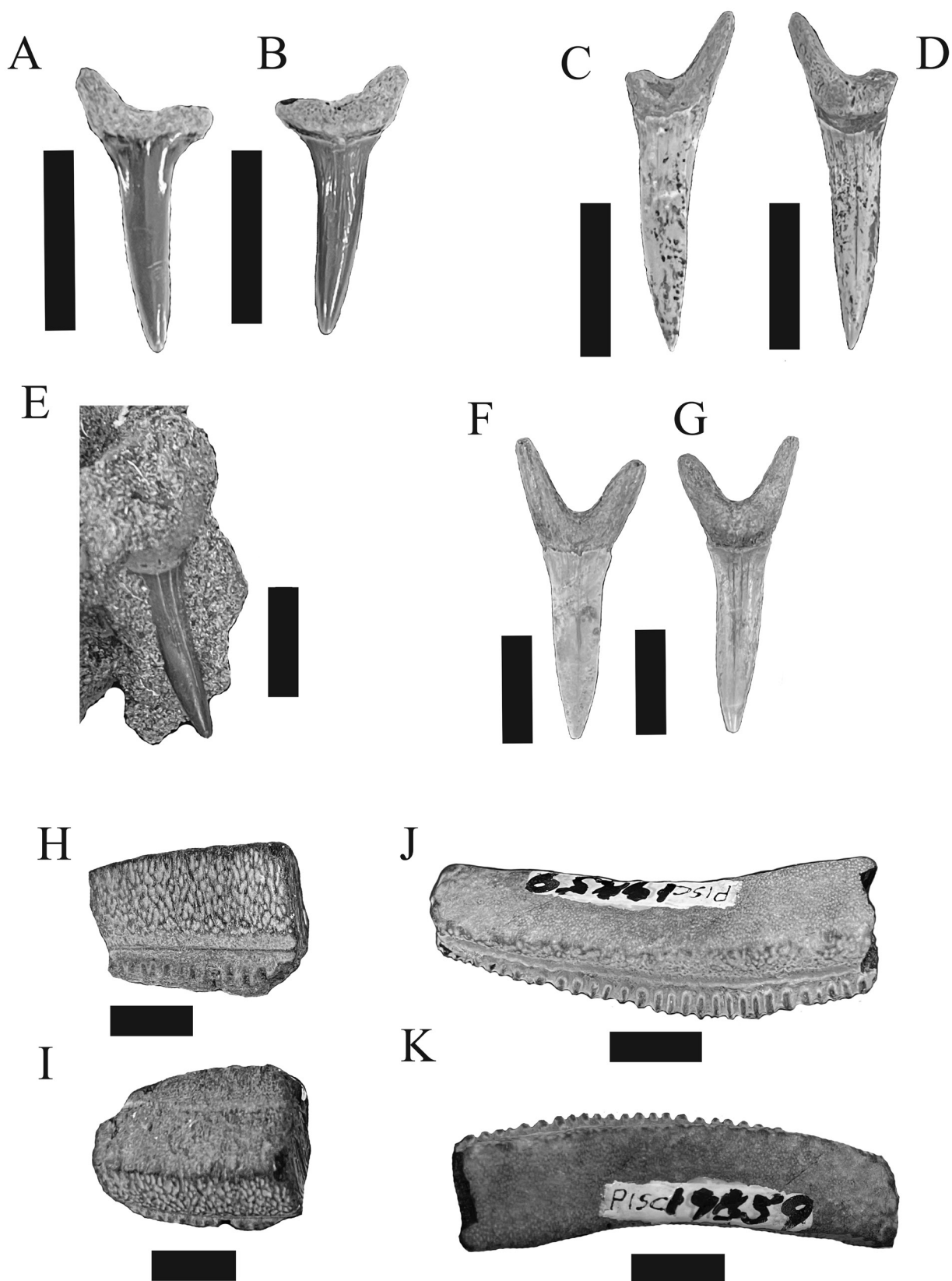


FIGURE 11. Paleocene chondrichthyan teeth from National Capital Parks East, Maryland. A-G), *Striatolamia* sp. teeth from the Aquia Formation from Fort Washington Park (FOWA) and Piscataway Park (PISC). A-B) FOWA 6186, A) labial, B) lingual. C-D) FOWA 11801, C) labial, D) lingual. E) FOWA 14824, lingually exposed tooth in matrix. F-G) PISC 24738, F) labial, G) lingual. H-K), *Rhinoptera* sp. teeth from the Aquia Formation. H-I) PISC 19813, H) labial, I) oral. J-K) PISC 19814, J) labial, K) oral. Scale equals 1 cm.

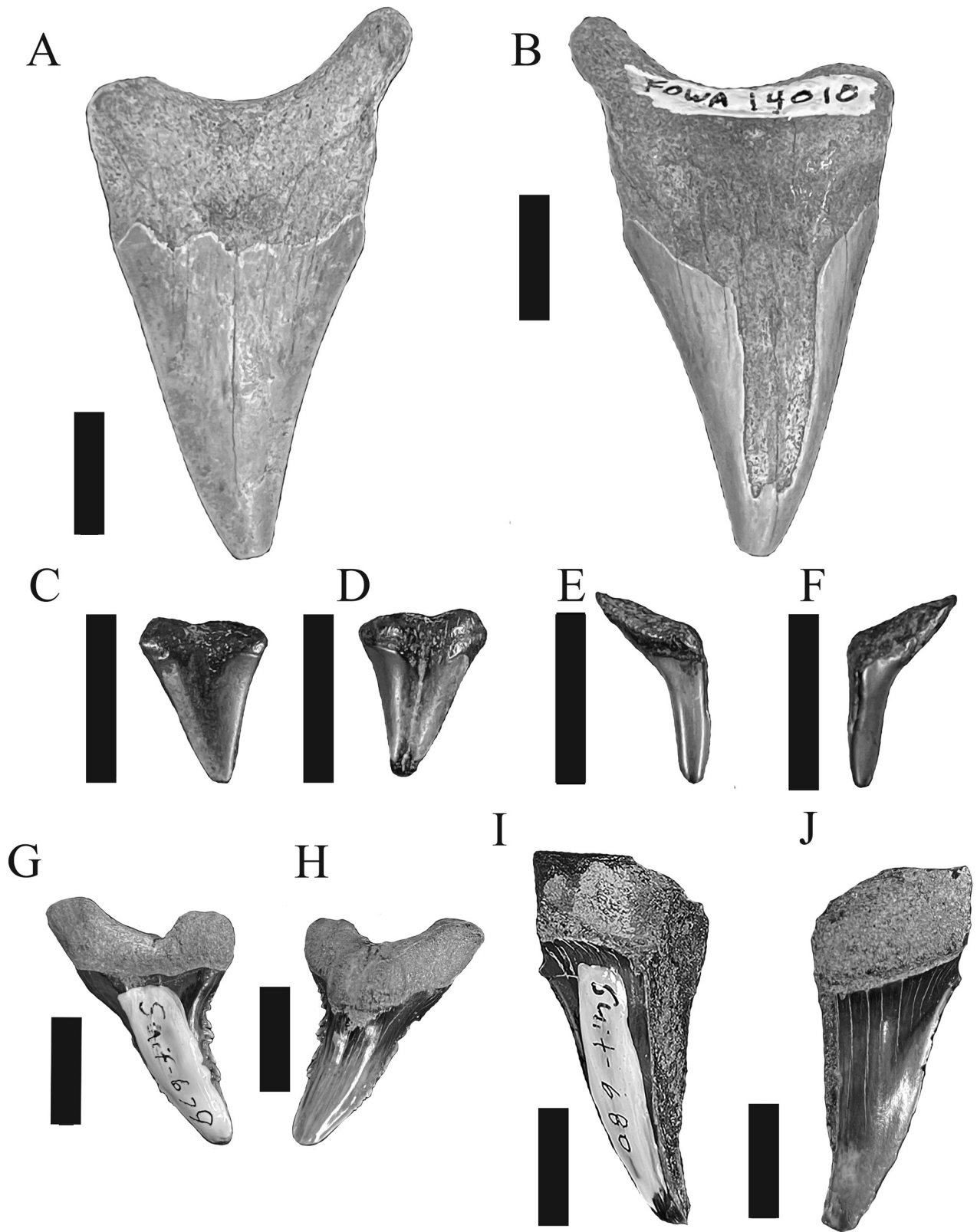


FIGURE 12. Miocene chondrichthyan teeth from the National Capital Parks East, Maryland. **A-B**) FOWA 14010, *Carcharodon* cf. *C. hastalis* tooth from possibly the Calvert Formation at Fort Washington Park, Maryland, **A**) labial, **B**) lingual. **C-F**) carcharhinid indeterminate taxa from possibly the Calvert Formation at Fort Washington Park, Maryland. **C-D**) FOWA 14012, **C**) labial, **D**) lingual. **E-F**) FOWA 14011, **E**) labial, **F**) lingual. **G-J**) Chondrichthyan teeth from the Calvert Formation at Suitland Parkway (SUIT), Maryland. **G-H**) SUIT 679, *Hemipristis serra*, anterolateral tooth, **G**) labial, **H**) lingual. **I-J**) SUIT 680, *Carcharodon hastalis*, tooth, **I**) labial, **J**) lingual. Scale equals 1 cm.

### Petersburg National Battlefield, Virginia (PETE)

#### Pliocene

*Yorktown Formation*—Two undiagnosed shark teeth were discovered in the lower Yorktown Formation of Petersburg National Battlefield in a core sample (Pranger, unpubl. report to PETE, 2000).

### Point Reyes National Seashore, California (PORE)

#### Miocene

*Santa Margarita Sandstone*—Pearson et al. (2016) reported the occurrences of isolated teeth of *Otodus megalodon*, *Carcharodon hastalis*, and *Hexanchus* sp. in the Santa Margarita Sandstone at PORE.

*Santa Cruz Mudstone*—Pearson et al. (2016) reported the occurrences of isolated teeth of *Otodus megalodon* in the Santa Cruz Mudstone at PORE.

#### Miocene/Pliocene

*Purisima Formation*—Bossenecker (2011) reported on a number of chondrichthyan fossils from the Upper Miocene to Lower Pliocene San Gregorio section of the Purisima Formation at PORE. These included isolated teeth of cf. *Hexanchus* sp., *Pristiophorus* sp., *Squatina* sp., *Cetorhinus maximus*, *Carcharodon carcharias*, *Carcharodon* sp., *Isurus oxyrinchus*, and cf. *Sphyrna* sp. (Bossenecker, 2011). Teeth, dermal denticles, and skeletal material of cf. *Raja binoculata* have also been collected from this horizon (Bossenecker, 2011).

#### Pliocene

*Drake Bay Formation*—Indeterminate shark teeth were collected amongst the remains of a whale skeleton from the Pliocene marine Drake Bay Formation at Point Reyes National Seashore (Galloway, 1977).

### Santa Monica Mountains National Recreation Area, California (SAMO)

#### Early Miocene

*Topanga Canyon Formation*—Koch et al. (2004) listed the presence of “shark gill-rakers”, most likely referring to the filtration denticles found in the gills of basking sharks, *Cetorhinus maximus*.

#### Middle–Late Miocene

*Modelo Formation*—Indeterminate shark teeth are reported from the Modelo Formation (Koch et al., 2004; Tweet et al., 2012).

### Vicksburg National Military Park, Louisiana–Mississippi (VICK)

#### Oligocene

*Vicksburg Group*—The lamniform *Otodus auriculatus*, which should be corrected to *Otodus angustidens* (V. Perez, per comm, 2022), was reported within Oligocene sediments in Vicksburg National Military Park, which also has reports of teeth of indeterminate sharks and rays (Kenworthy et al., 2007).

## DISCUSSION AND CONCLUSIONS

As demonstrated above there are at least forty-six National Park Service units with a record of fossil chondrichthyans present within or very close to their respective park boundaries (Fig. 1). These NPS chondrichthyan sites span at least 360 million years of evolutionary history, and representatives of all the major chondrichthyan groups represented throughout geologic time have been found in at least one NPS site. A summary of the occurrences of chondrichthyan fossils throughout the National Park Service system shows that the majority of Paleozoic chondrichthyan NPS sites are located in the interior of the United

States, often exposed in canyons, mountain, and cave localities. The majority of these Paleozoic chondrichthyan sites represent Middle to Late Mississippian or Early to Middle Permian assemblages. The Mesozoic NPS record of chondrichthyans are largely constrained to the Late Cretaceous, representing the assemblages that occurred in association with the Cretaceous Interior Seaway. The exception for the Mesozoic is the Late Triassic assemblages of chondrichthyans found at PEFO. For the Cenozoic, a few NPS sites have Paleocene and Eocene assemblages including the inland freshwater lake rays found at FOBU and a few coastal assemblages found at FOWA and PISC. The majority of the Cenozoic chondrichthyan assemblages are found along coastal parks and represent coastal marine assemblages from the Miocene to the Pleistocene. However, in many cases, these Cenozoic NPS sites have not been rigorously studied because more accessible and extensive outcrops exist outside the bounds of NPS lands.

Although this review establishes a rich record of sharks and other chondrichthyans occurring within National Park Service areas, the majority of the chondrichthyan assemblages have not yet been fully described, or even identified beyond a reference to “fossil shark teeth”. A large amount of work is needed to bring these chondrichthyan assemblages to light for scientific contributions and educational outreach. For palaeoichthyology and paleontology overall, the lands of the National Park Service are a time capsule that has the potential to yield valuable data and insight for not only the life history of our ancient shark heritage in America, but for all ancient organisms that lived and evolved on this dynamic planet.

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