THE OCCURRENCE OF THE MIDDLE MISSSISSIPPIAN *CARCHAROPSIS WORTHENI* (CHONDRICHTHYES, EUSELACHII) AT DEATH VALLEY NATIONAL PARK, CALIFORNIA

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Abstract—An isolated tooth of *Carcharopsis wortheni* was collected from the Middle Mississippian (Visean) Mexican Springs Formation of the Perdido Group at Death Valley National Park, California by USGS staff in 1963. This marks the first record of this euselachian chondrichthyan taxon for both California and Death Valley National Park and the first description of a Late Paleozoic vertebrate from Death Valley. This specimen also represents the westernmost occurrence of *C. wortheni* in North America. A review of the known records of *C. wortheni,* mapped on a reconstruction of Middle Mississippian North America paleogeography, indicates *Carcharopsis* was a rare apex predator in the Middle Mississippian marine fish assemblages but had a wide distribution along the southern and western coast of the sub-continent Laurentia.

INTRODUCTION

Death Valley National Park (DEVA) consists of 3,373,063 acres along the California–Nevada border, including parts of both the Great Basin and Mojave deserts, and preserves a rich fossil record (Nyborg and Santucci, 1999). The fossils found here span from the Proterozoic to the Holocene (Nyborg and Santucci, 1999). The Paleozoic vertebrate record at DEVA is best known from Devonian sites that are dominated by fossil fish remains. The earliest report of Devonian fish from DEVA was by Dunkle and Lane (1971) who reported a right posterior dorsolateral and left interolateral plates of *Dunkleosteus terrelli*, a cladodont-grade chondrichthyan tooth, and a possible holocephalan chondrichthyan tooth from the Quartz Spring Sandstone Member of the Lost Burro Formation. Snow (1990) later marked the presence of Early Devonian vertebrate fossils from the Lippincott Member of the Lost Burro Formation in the east-central part of the Panamint Mountains. Subsequently, a number of agnathan taxa were described from this geologic horizon (Elliott and Ilyes, 1993, 1996; Elliott and Petriello, 2011; Elliott, 2016). Few vertebrate fossils have been identified from the Carboniferous rocks at DEVA. Stone et al. (2014, p. 8, fig 3D) figured a nearly complete ctenacanthiform spine from the Marble Canyon region in the Late Mississippian Indian Springs Formation (Serpukhovian). This spine was not collected or identified to a specific taxon. Here we report on the first occurrence of a Middle Mississippian (Visean) vertebrate fossil from the Perdido Group (Mexican Spring Formation) at DEVA, and the westernmost occurrence of the chondrichthyan, *Carcharopsis wortheni*, in North America.

MATERIALS AND METHODS

The specimen presented here was collected in 1963 by USGS staff and is reposited in the Paleobiology Department Fossil Fish Collection at the National Museum of Natural History, Washington D.C. The specimen was photographed using a Nikon W150 camera and measured with digital calipers. Figures were edited and generated with Adobe Photoshop and Adobe Illustrator respectively. **Institutional Abbreviation**: **USNM**, National Museum of Natural History, Washington D.C.

GEOLOGIC SETTING

The specimen presented here was originally listed as being collected from the Mississippian Perdido Formation in the northwest region of DEVA, near Rest Spring (Fig. 1) (McAllister, 1952). Stevens et al. (1996) revised the local stratigraphic nomenclature and raised the Perdido Formation to a group. The Perdido Group (Fig. 2) lies stratigraphically above the Tin Mountain Limestone (older) and below the Rest Spring Shale (younger) and includes two formations, the Leaning Rock Formation and overlying Mexican Spring Formation (Stevens et al., 1996). Based on the locality information with the specimen we tentatively suggest that this specimen derived from the Mexican Spring Formation, as it is the dominant geologic unit exposed in the area. The Mexican Spring Formation also consists of rocks originally assigned to the Perdido Formation (Stevens et al., 1996). The Mexican Spring Formation consists of siltstones and fine-grained sandstones, suggesting deep water deposition (Stevens et al., 1996). Fossils from the Mexican Spring Formation include conodonts, brachiopods, and ammonoids of Meramecian (Visean) age (Stevens et al., 1996).

SYSTEMATIC PALEONTOLOGY

CLASS Chondrichthyes Huxley, 1880
SUBCLASS Elasmobranchii Bonaparte, 1838
COHORT Euselachii Hay, 1902
FAMILY *incertae sedis*
GENUS *Carcharopsis* Agassiz, 1843
Carcharopsis wortheni Newberry, 1866

Occurrence—Mexican Springs Formation, Middle Mississippian (Visean); Death Valley National Park, California.

Material—USNM 23108, single tooth in a sedimentary rock fragment.

Description—Part of a large tooth, preserving the median cusp and the mesio-medial portions of the tooth base, with preserved base width of 4 cm wide and a crown height of 4 cm (Fig. 3). The tooth is exposed labially with the distal portion of the tooth missing. The median cusp is triangular and mesio-distally broad near the base of the cusp. Pronounced serrations are present on the carina of the median cusp with some serrations bearing minute secondary serrations. The mesial lateral cusp is only partially visible. Small minute cusplets are present on the mesial portion of the tooth between the median and lateral cusps. The tooth base is only partly exposed on its labial side, indicating a thin platform for the tooth base. The lingual margin of the base is not exposed.

Remarks— At present, there are four species of *Carcharopsis* recognized; *C. prototypus* (type species), *C. okensis*, *C. yerofeyewi*, and *C. wortheni*. Ginter et al. (2010) list

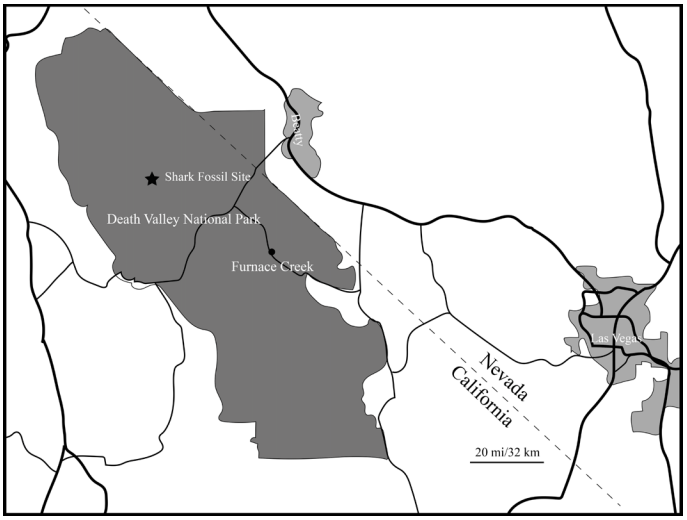


FIGURE 1. The approximate locality of the shark fossil site (star) within Death Valley National Park, California.

also *C. dentatus* but suggest that it is a junior synonym of *C. prototypus*. Of these four species, only *C. wortheni* is known from North America, the other three are primarily Eurasian in distribution (Ginter et al., 2010). *Carcharopsis wortheni* was first described by Newberry (*in* Newberry and Worthen 1866) from a single tooth collected from "Sub-Carboniferous limestone, Huntsville, Alabama". It was noted that the tooth had some similarities to teeth of *Cladodus*, particularly the tooth base with the lingual torus being semi-circular and a flatten labial margin, but differed in having a much broader and coarsely serrated median cusp. Eastman (1917) named "*Dicrenodus texanus*" (USNM 8097) from "strata of Pennsylvanian age" near San Saba, Texas. This specimen and taxon are considered synonymous with *C. wortheni* (Ginter et al., 2010; Bronson et al., 2018). Up until the mid-1980s, most of what was known about *C. wortheni* was based on isolated teeth (Zangerl, 1981). Lund and Mapes (1984) described jaws and the isolated tooth of *C. wortheni* from the Late Mississippian Fayetteville Formation in northwestern Arkansas. Additional skeletal material, including a chondrocranium with jaws and a number of teeth of *C. wortheni,* were described from the Fayetteville Formation in Arkansas by Bronson et al. (2018). This new material demonstrated that *Carcharopsis* had a chondrocranium with features found in euselachian chondrichthyans (hybodontiforms and neoselachians), suggesting that *Carcharopsis* may have been a basal member of this clade (Bronson et al., 2018). The structure of the jaws and the enameloid of its serrated teeth suggest that *Carcharopsis* was an apex predator with a powerful shearing bite (Lund and Mapes, 1984; Duffin and Cuny, 2008).

DISCUSSION AND CONCLUSIONS

In reviewing the distribution of the records of *Carcharopsis wortheni* in North America, we plotted the known published records of *C. wortheni* onto a palaeogeographical reconstruction of North America during the Middle–Late Mississippian (Visean–Serpukhovian) (Fig. 4). In addition to the type specimen of *C. wortheni* in northern Alabama and the fossils from the Fayetteville Formation, we also included data from Ciampaglio et al. (2011), in which they identified additional specimens of *C. wortheni* from northern Alabama in the Hartselle Limestone, Monteagle Limestone, and Pride Mountain Limestone. Grogan et al. (2012) and Lund et al. (2015) list the occurrence of *Carcharopsis* at the Late Mississippian (Serpukhovian) Bear Gulch Limestone fish assemblage in the Heath Formation of central Montana; but have not yet described these specimens. We tentatively added the *C. wortheni* tooth from the San Saba

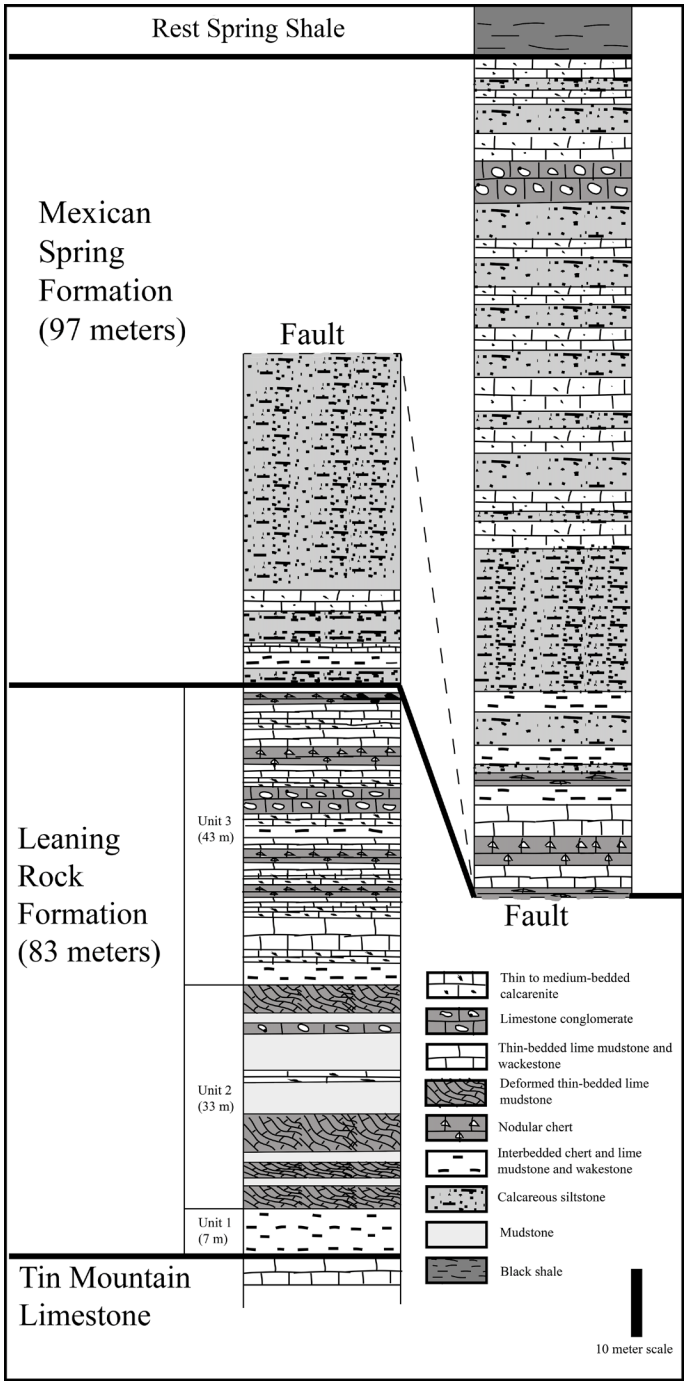


FIGURE 2. The stratigraphy of the type section of the Leaning Rock Formation and reference section of the Mexican Spring Formation (Perdido Group) in the Quartz Spring region of Death Valley National Park, California (redrawn from figure 8, in Stevens et al., 1996).

region of Texas to this map as well. Though Eastman (1917) listed the specimen as coming from Pennsylvanian rocks, he was unable to provide specific geologic context and it is probable that this specimen is from a Mississippian-age formation. We have also added additional unpublished data that include a tooth associated with skeletal cartilages within a limestone nodule from the Barnett Formation (Late Mississippian, Serpukhovian) of the House Canyon region of west Texas, which is currently under study by the lead author (JPH along with W. Itano and L. Lambert), and isolated teeth from the Bangor Limestone at Tumbling Rock Cave, Alabama and Rumbling Falls Cave,

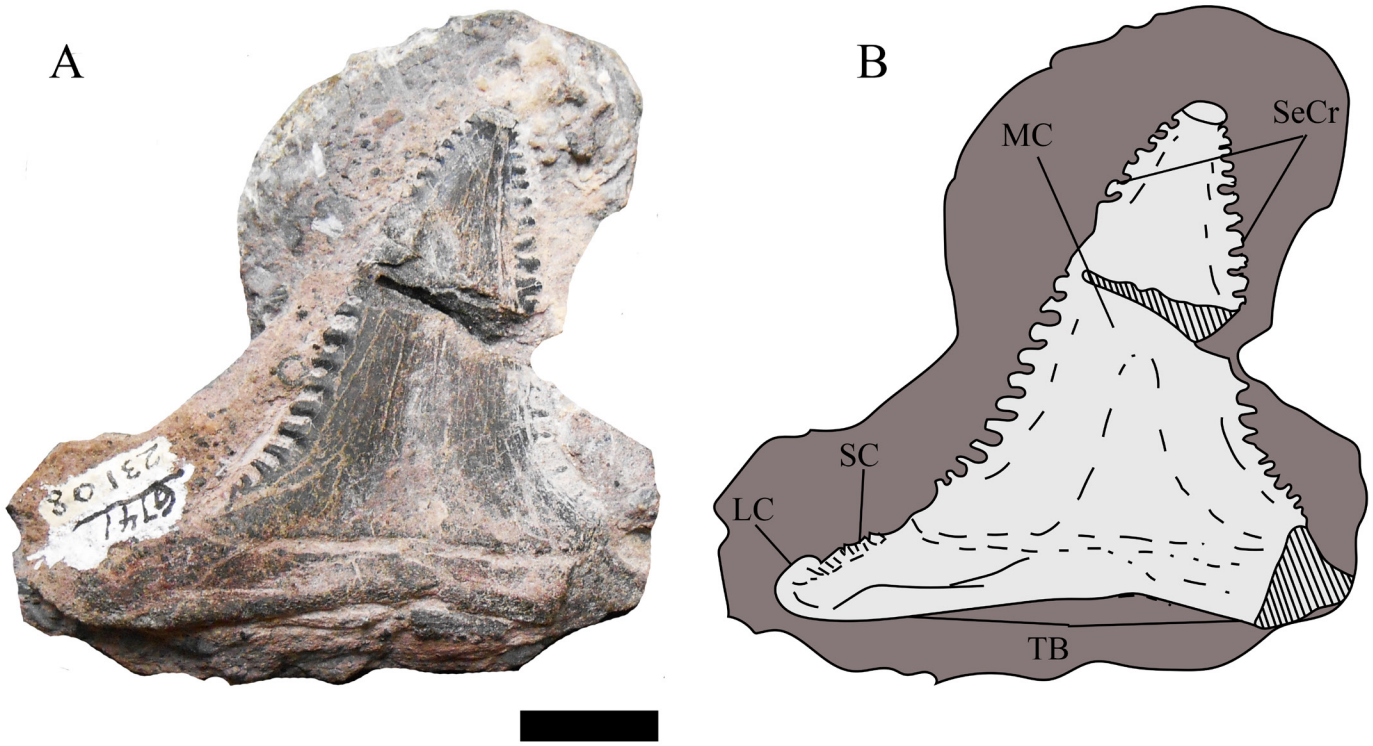


FIGURE 3. USNM 23108, tooth of *Carcharopsis wortheni* from Death Valley National Park. **A**) photo of specimen in labial view. **B**) line diagram of anatomical features of the specimen; **LC**, lateral cusp, **MC**, median cusp, **SC**, secondary cusplets, **SeCr**, serrated carina, **TB**, tooth base. Scale equals 1 cm.

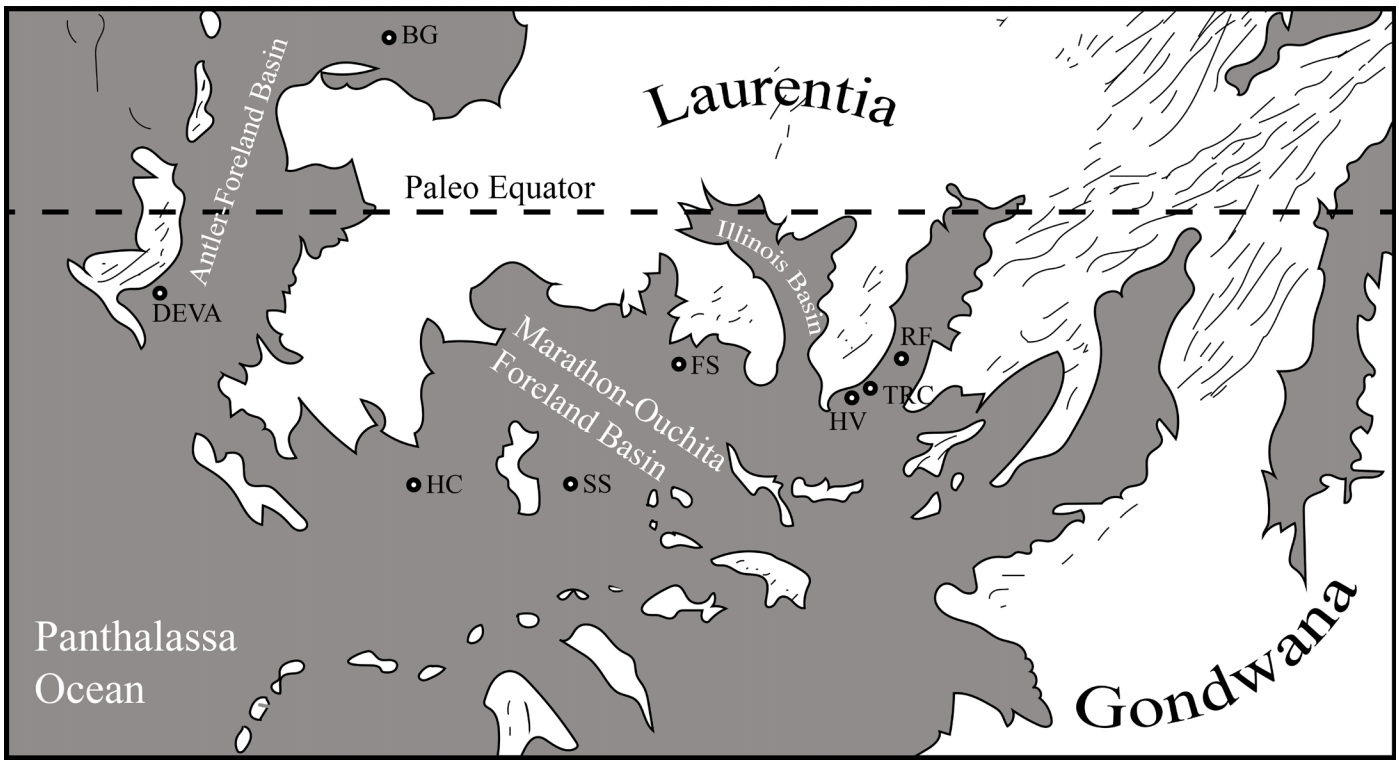


FIGURE 4. The Middle–Late Mississippian (Visean–Serpukhovian) paleogeographic distribution of *Carcharopsis wortheni*, in lower North America. Abbreviations: **BG**, Bear Gulch Limestone, Heath Formation (Serpukhovian), Montana; **DEVA**, Death Valley National Park, Mexico Springs Formation (?Visean), California; **FS**, Fayetteville Shale (Serpukhovian), Arkansas; **HC**, House Canyon, Barnett Formation (Visean/Serpukhovian), West Texas; **HV**, Huntsville region , Hartselle Limestone, Monteagle Limestone, and Pride Mountain Limestone (Serpukhovian), Alabama; **RF**, Rumbling Falls, Bangor Formation (Serpukhovian), Tennessee; **SS**, San Saba, unknown formation (Late Mississippian/Early Pennsylvanian?, Texas; **TRC**, Tumbling Rock Cave, Bangor Formation (Serpukhovian), Alabama. Figure redrawn from original map by R. Blakey (https://deeptimemaps.com/).

Tennessee (R. Saker, personal commun., 2021).

The distribution of *Carcharopsis wortheni* shows that this taxon had an extensive range in the marine basins south of the paleoequator, the exception being the Bear Gulch Limestone assemblage which had a northern latitudinal position (Grogan et al, 2012; Lund et al., 2015). There presently seems to be a higher concentration of records of *C. wortheni* towards the eastern waters, in the marine basin that encompassed eastern Alabama and Tennessee (Newberry and Worthen, 1866; Ciampaglio et al., 2011; R. Saker, personal commun.). West of this basin, the Fayetteville Formation sites in northwestern Arkansas seem to be the next highest concentration of *C. wortheni* specimens that include skeletal material (Lund and Mapes, 1984; Bronson et al., 2018). The Texas records of *Carcharopsis* are sparse with only two specimens known (Eastman, 1917; JPH, personal obs.), and the specimen from DEVA is the westernmost location of *C. wortheni* within these waters. Most of the specimens reported here come from Middle–Late Mississippian (Visean–Serpukhovian) age localities, most of which are Serpukhovian in age. The *Carcharopsis* tooth described by Eastman (1917) from San Saba, Texas was reported to have been collected from Pennsylvanian-age rocks, although as stated above these rocks could have been incorrectly dated or identified considering the state of knowledge of the local geology at the time. However, Itano and Lucas (2014) proposed that a tooth fragment previously referred to the eugenodontiform *Edestus* from the Pennsylvanian Aoertu Formation in China (Cheng et al., 1996) may in fact be a fragmentary specimen of *Carcharopsis* due to the lack of bilateral symmetry and the presence of a lateral cusp in the specimen. If this identification holds true, then the occurrence of *Carcharopsis* in Pennsylvanian beds of North America is plausible.

In conclusion, from the collectively few specimens known of *Carcharopsis wortheni* found in North America, it appears that this early euselachian taxon was a rare apex predator component of Middle–Late Mississippian marine fish assemblages, but had a wide distribution along the southern and western coast of the Laurentia sub-continent of Pangea. The record of *Carcharopsis wortheni* from the Middle Mississippian Mexican Springs Formation and of the ctenacanthiform spine in the Marble Canyon region in the Indian Springs Formation (Stone et al., 2014) at DEVA demonstrates the potential of significant Late Paleozoic vertebrate assemblage records within the park. Further work at DEVA could help provide new information for Late Paleozoic vertebrates of western North America, of which little is known today.

ACKNOWLEDGMENTS

We are indebted to the hospitality and assistance of Amanda Millhouse of the Paleobiology Collections at the National Museum of Natural History who arranged for us to have access to the fossil fish collections. We thank Nancy Stamm from the USGS for providing background information on the specimen presented here. We are also highly appreciative of Rachel Saker of the Southeastern Cave Conservancy (SCC), who provided us information on new records of *Carcharopsis wortheni* within cave sites in Tennessee and Alabama. We also appreciate data from Wayne Itano and Lance Lambert on the new *Carcharopsis* specimen from House Canyon, Texas. We thank Dave Elliott and Wayne Itano for reviewing this manuscript; their notes and edits greatly improved this manuscript.

REFERENCES

Bronson, A.W., Mapes, R.H., and Maisey, J.G., 2018, Chondrocranial morphology of *Carcharopsis wortheni* (Chondrichthyes, Euselachii incertae sedis) based on new material from the Fayetteville Shale (Upper Mississippian, Middle Chesterian): Papers in Paleontology, v. 4, p. 349-362.

Cheng, Z., Lucas, S.G., and Zidek, J., 1996, *Edestus* (Chondrichthyes, Elasmobranchii) from the Upper Carboniferous of Xinjiang, China: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1996 (11), p. 701-707.

Ciampaglio, C.N., Deuter, L.H., Taylor, M.A., and Cicimurri, D.J., 2011, A review of the chondrichthyans from the Mississippi System of northern Alabama, USA: Bulletin of the Alabama Museum of Natural History, v. 28, p. 67-80.

Duffin, C.J. and Cuny, G., 2008, *Carcharopsis prototypus* and the adaptations of single crystallite enameloid in cutting dentitions: Acta Geologica Polonica, v. 58, p. 181-184.

Dunkle, D.H. and Lane, N.G., 1971, Devonian fishes from California: Kirtlandia, v. 15, p. 1-5.

Eastman, C.R., 1917, Fossil fishes in the collection of the United States National Museum: Proceedings of the United States National Museum, v. 52, p. 235-304.

Elliott, D.K., 2016, The Boothiaspidinae, a new agnathan subfamily (Heterostraci, Cyathaspididae) from the late Silurian and Early Devonian of the western United States and the Canadian Arctic: Journal of Paleontology, v. 6, p. 1212-1224.

Elliott, D.K., and Ilyes, R.R., 1993, Lower Devonian vertebrates from the Lippincott Member of the Lost Burro Formation in Death Valley National Monument; in Santucci, V. L., ed., 3rd Fossil Resources Conference, Fossil Butte National Monument, Wyoming. 1992, National Park Service Paleontological Research Abstract Volume 1, Technical Report NPS/NRPEFO/NRTR-93/11, p. 20.

Elliott, D.K., and. Ilyes, R.R., 1996, New Early Devonian pteraspidids (Agnatha, Heterostraci) from Death Valley National Monument, southeastern California: Journal of Paleontology, v. 70, p. 152–161.

Elliott, D.K., and Petriello, M.A., 2011, New poraspids (Aganatha, Heterostraci) from the Early Devonian of the western United States: Journal of Vertebrate Paleontology, v. 31, p. 518-530.

Ginter, M., Hampe, O., and Duffin, C.J., 2010, Chondrichthyes. Paleozoic Elasmobranchii: Teeth, *in* Schultze, H.-P., ed., Handbook of Paleoichthyology, v. 3D, München, Verlag Dr. Friedrich Pfeil, 168 p.

Grogan, E.D., Lund, E.D., and Greenfest-Allen, E., 2012, The origin and relationship of early chondrichthyans; *in* Carrier, J.C., Musick, J.A., and Heithaus, M.R., eds., Biology of Sharks and Their Relatives, Edition 2, p. 3-29.

Itano, W.M. and Lucas, S.G., 2014, The youngest record of *Carcharopsis* (Chondrichthyes) from the Pennsylvanian of Xinjiang Uyghur Autonomous Region, China: Paleoworld, v. 23, p. 258-262.

Lund, R. and Mapes, R.H., 1984, *Carcharopsis wortheni* from the Fayetteville Formation (Mississippian) of Arkansas: Journal of Paleontology, v. 58, p. 709-717.

Lund, R., Greenfest-Allen, E. and Grogan, E.D., 2015, Ecomorphology of the Mississippian fishes of the Bear Gulch Limestone (Heath Formation, Montana, USA): Environmental Biology of Fishes, v. 98, p. 739–754.

McAllister, J.F., 1952, Rocks and structures of the Quartz Spring area, northern Panamint Range, California: California Division of Mines Special Report, no. 25, 38 p. (incl. geologic map, scale 1:19,200).

Newberry, J.S. and Worthen, A.H., 1866, Descriptions of new species of vertebrates, mainly from the Subcarboniferous limestone and coal measures of Illinois: Geological Survey of Illinois II, p. 9-131.

Nyborg, T.G., and Santucci, V.L., 1999, The Death Valley National Park paleontological survey. National Park Service, Geological Resources Technical Report, NPS/NRGRD/GRDTR-99/01.

Snow, J.K., 1990, Cordilleran orogenesis, extensional tectonics and geology of the Cottonwood Mountain area, Death Valley region, California and Nevada [Ph.D. dissertation]: Harvard University, Cambridge, Massachusetts, 210 p.

Stevens, C.H., Klingman, D.S., Sandberg, C.A., Stone, P., Belasky, P., Poole, F.G. and Snow, J.K., 1996, Mississippian stratigraphic framework of east-central California and southern Nevada with

revision of Upper Devonian and Mississippian Stratigraphic units in Inyo County, California: U.S. Geological Survey, Bulletin 1988-J. 39 p.

Stone, P., Stevens, C.H., Belasky, P., Montanez, I.P., Martin, L.G., Wardlaw, B.R., Sandberg, C.A., Wan, E., Olson, H.A. and Priest, S.S., 2014, Geologic map and upper Paleozoic stratigraphy of the Marble Canyon area, Cottonwood Canyon quadrangle, Death Valley National Park, Inyo County, California: Pamphlet to accompany U.S. Geological Survey Scientific Investigations Map 3298, scale 1:24,000, 59 p., http://dx.doi.org/10.3133/sim3298. ISSN 2329–132X (online).

Zangerl, R., 1981, Chondrichthyes I. Paleozoic Elasmobranchii; *in* Schultze, H.-P., ed., Handbook of Paleoichthyology 3A: Stuttgart, New York, Gustav Fischer, 115 p.

