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RESEARCH ARTICLE

SAIVODUS STRIATUS (CHONDRICHTHYES, CTENACANTHIFORMES) FROM THE LOWER CARBONIFEROUS OF SOUTHWESTERN VIRGINIA

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ABSTRACT

The Lower Carboniferous is represented in southwestern Virginia and northeastern Tennessee as a narrow band of mostly marine sedimentary rocks approximately 135 km long and represents a series of transgressive and regressive sea-level episodes. Only one vertebrate has been recorded from these strata (a now lost specimen of "*Cladodus*" collected from Hancock County, east Tennessee in the mid-Twentieth Century) prior to the current report. *Saivodus striatus* (Chondrichthyes, Ctenacanthiformes) is herein described for the first time from the state of Virginia, more than 350 km from its closest known occurrence. These chondrichthyans are some of the latest records of marine vertebrates from the Rheic Ocean during its closure in advance of the Alleghenian Orogeny and subsequent uplift of Paleozoic strata in the southern Appalachians.

Keywords: Carboniferous, Chondrichthyes, Ctenacanthiformes, *Saivodus striatus*, Southwestern Virginia.

INTRODUCTION

Paleozoic sedimentary units make up much of the southern Appalachian region. These rocks offer an extensive record of marine ecosystems and tectonic movements from the Cambrian through Carboniferous Periods (Horton et al., 1989). During the latter part of the Paleozoic, the Iapetus and Rheic Oceans were encroached upon and ultimately ablated by approaching continental landmasses, coincident with the formation of the singular, Panthalassic Ocean (Beaumont et al., 1987). After the Serpukhovian Stage (330 Ma), sedimentary units in the region

were primarily terrestrial and freshwater, yielding rich coal-bearing deposits from these ancient ecosystems (Butts, 1940).

Thus, the Lower Carboniferous rocks from these localities are important records of past life in a time of great ecological change. Though the sedimentary rock record from this time is immense (Ettensohn et al., 2022), few vertebrates have been described. Vertebrate remains must occur in these units and are either as-yet undiscovered, or they already exist in museum collections and are awaiting description. Described here is one such specimen collected in 1975, a ctenacanthiform chondrichthyan tooth from southwestern Virginia.

The Lower Carboniferous (Tournaisian – Serpukhovian) is represented in southwestern Virginia and northeastern Tennessee as a narrow (~2-4 km) band of mostly marine sedimentary rocks approximately 135 km long and is made up (from oldest to youngest) of the Grainger, MacCrady-Price, Newman (Greenbrier), and Pennington Formations, and represents a series of transgressive and regressive sea-level episodes (Ettensohn et al., 2022). These units are extensive throughout the Appalachian Plateau of the southern Appalachians but are found in the Ridge and Valley physiographic province only in Smyth, Washington, Scott, and Lee Counties in Virginia (Butts, 1940), and Hawkins and Hancock Counties (Greene, 1959) in Tennessee (Fig. 1). Shallow marine sandstones, shales, and carbonates, along with terrestrial and freshwater deposits reflect a disappearing ocean environment (Butts, 1940). Though the units are stratigraphically contiguous in southwestern Virginia and northeastern Tennessee, different names are applied to the units in each of the States and regions where they are found and introduces nomenclatural ambiguity (Fig. 1 includes unit names used previously in Tennessee and Virginia). These marine rocks (and the fossils therein) preserve some of the latest records of the Rheic Ocean during its closure in advance of the Alleghenian Orogeny and subsequent uplift and deformation of Paleozoic strata in the southern Appalachians.

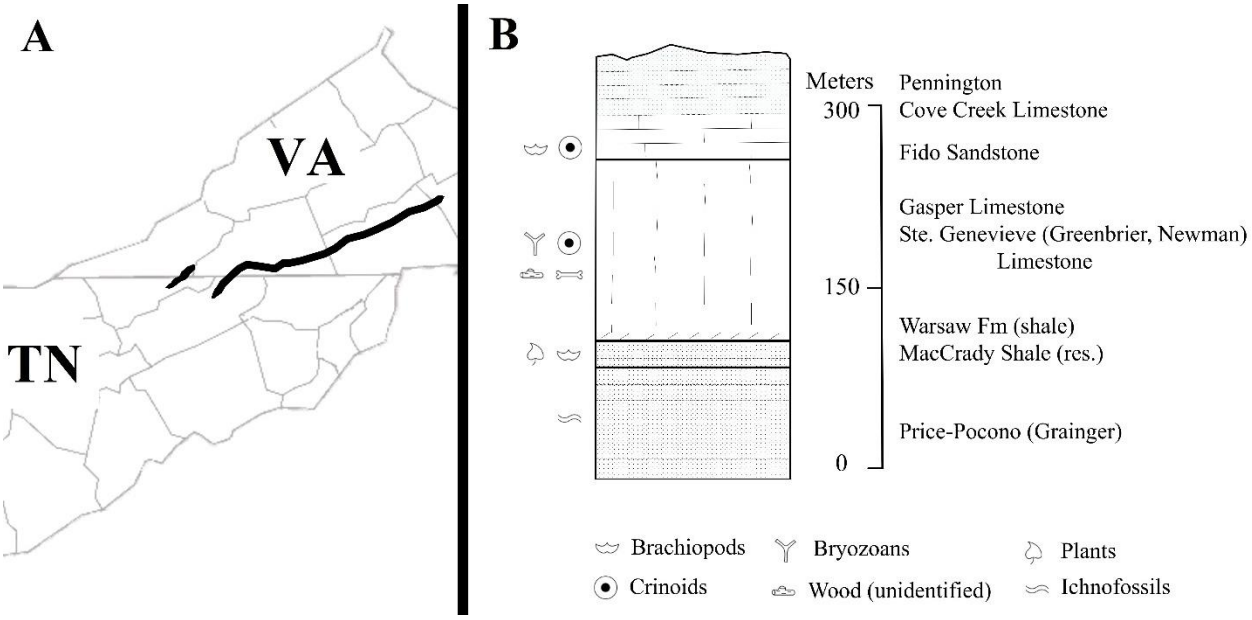

Figure 1. (**A**) Early Carboniferous rock units in southwestern Virginia and northeastern Tennessee; (**B**) stratigraphic sequence of the lower Carboniferous units discussed herein and fossils noted (stratigraphic column based on Greene, 1959 and Ettensohn et al., 2022).

Greene (1959) reported the only vertebrate known from these exposures (before the current report), a single tooth of "*Cladodus*" from the Newman Limestone of Hancock County, Tennessee (which was discussed briefly in Corgan & Breitburg, 1996). That specimen is now lost and was not figured in the work in which it was reported, and could be *Cladodus* as reported, or any of several other cladodont-grade tooth taxa historically placed in *Cladodus* (see Duffin and Ginter, 2006 for a review of the genus and its current diagnosis), or another chondrichthyan with similar morphology (Ginter et al., 2010) entirely.

MATERIAL

Chondrichthyes Huxley, 1880
Ctenacanthiformes Glikman, 1964
Ctenacanthidae Dean, 1909
Saivodus Duffin and Ginter, 2006
Saivodus striatus Agassiz, 1843
(Fig. 2)

Description. EH23 (Fig. 2) is a partial chondrichthyan tooth found in 1975 along US Highway 611 in southwestern Virginia by P. Helm during an Emory and Henry College geology class field trip and later donated to the Museum of the Middle Appalachians. Highway 611 lies along the unconformity between the Lower Carboniferous Greenbrier and MacCrady Formations for most of its length in southwestern Virginia. EH23 measures 17.25 mm along its mesiodistal length from the preserved portion of the tooth base to the distal point of the median cusp; the median cusp is 14.7 mm in height. It is preserved in labial view and is embedded in a block of light brown, shaly matrix that measures approximately 2.5 by 3.5 cm (which contains other vertebrate fossils *incertae sedis*). EH23 is referred to *Saivodus* by its relatively large size and longitudinal cristae comprising the proximal two thirds of the median cusp. It is further referred to *S. striatus* by the sigmoid curvature of the median cusp, the basal width of which equals three tenths of its length, making it belong to the slender morphotype which further implies that it occupied an anterior position within the oral cavity (Duffin & Ginter, 2006). This could also explain the apparent lack of accessory cusplets, though the state of preservation of EH23 could also have ablated any accessory cusplets if originally present.

Additional fossil material is also present on the EH23 matrix and is preserved as darker brown inclusions on the lighter colored matrix. Most are too incomplete to adequately diagnose, but a fragment along the upper left margin (as viewed labially) is intriguing. The deeply furrowed costae noticeable on the fragment is consistent with it being a portion of one of the two ossified dorsal fin spines characteristic of the Ctenacanthidae (Glikman, 1964). This morphology is also consistent with portions of the lateral cusp and accessory cuspids characteristic of many ctenacanthids, though its certain anatomical identification is not attempted here.

Remarks. Duffin and Ginter (2006) listed the distribution of *S. striatus* as the Upper Mississippian of Ireland, Scotland, England, Belgium, Morocco, and in the USA, Alabama, Arkansas, Indiana, Iowa, Missouri, and possibly Montana. It has since been reported from Austria (Feichtinger et al., 2021) and Kentucky, USA (Hodnett et al., 2022). This report adds to its geographic distribution and is more than 350 km from its closest locality in Kentucky.

Unsuccessful attempts were made by the author to locate the provenience of EH23 and the cladodont tooth from Greene (1959). Lower Carboniferous sedimentary samples were collected

from road cuts along US Highway 611 in Smyth, Washington, and Scott Counties in Virginia, and State Highways 70 and 33 in Hawkins and Hancock Counties, Tennessee, representing mostly the Greenbrier (Newman) Limestone, but also samples from the Grainger, MacCrady and Fido Formations were collected.

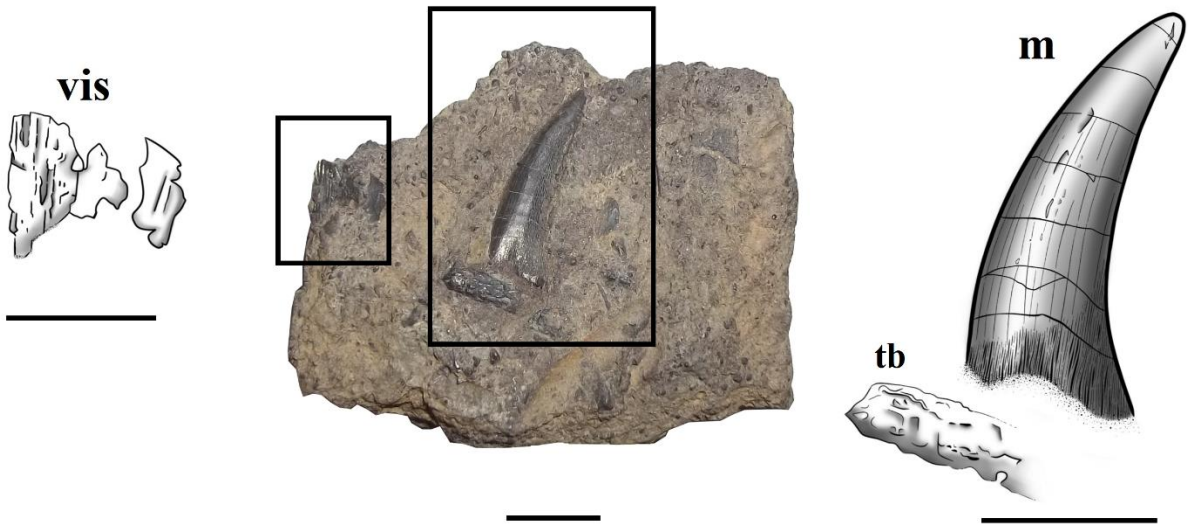

Figure 2. *Saivodus striatus* from southwestern Virginia (EH23) preserved in matrix in labial view with interpretive line drawings. Abbreviations: **m**, median cusp; **tb**, tooth base; **vis**, Vertebrata *incertae sedis*. Scale in each equals 5 mm. Line drawings courtesy of S. Koscielniak.

Macrofossils were abundant at several of the localities and illustrate a thriving marine ecosystem (especially noted at exposures of the Newman and Greenbrier Limestones). The trace fossils *Palaeophycus* and *Thalassinoides* were found in the Grainger Formation. Some exposures of the MacCrady Shale contained abundant brachiopods and one contained external casts of the plants *Calamites* and *Lepidodendron*. The Greenbrier Limestone contained several exposures with numerous invertebrates including bryozoans, crinoids, and brachiopods. One sample from the Fido Sandstone yielded crinoid stems and a single brachiopod mold. Carbonates from all localities were dissolved in buffered 6% acetic acid and the dried precipitates screened through USA Standard Testing Sieve sizes 10, 35, and 80 respectively. Few vertebrate microfossils have been recovered, but one sample of Greenbrier Limestone has produced a few vertebrate fragments *incertae sedis*. These lithological samples and their fossils are housed at the Nature Center at Steele Creek Park.

DISCUSSION

Are Paleozoic Chondrichthyans Sharks?

Though not an issue specific to this report, a matter of etymology warrants brief discussion. The term “shark” is ubiquitous in the literature to describe any fusiform, predatory chondrichthyan, including nearly all Paleozoic forms (e.g., Ginter et al., 2005; Maisey, 2007; Tomita, 2015; etc.). Indeed, “shark” may seem an axiomatic term for predatory marine chondrichthyans and be an adequate label for that ecomorph. Problems arise, however when we try to apply that ecological

label to extant elasmobranchs; would Whale Sharks, *Rhincodon typus* (A. Smith, 1828), or Basking Sharks, *Cetorhinus maximus* (Gunnerus, 1765), fit under that usage? What about members of the Batoidea (rays and skates), who (as members of Neoselachii) are more closely related to extant sharks than is any Paleozoic form (Maisey, 2012)?

"Shark" then, does not refer to all chondrichthyans, or even neoselachians, and the fusiform high-tier predator ecomorph has evolved multiple times in Chondrichthyes, such as in *Saivodus striatus* and its relatives (Grogan and Lund, 2012). The case is made here that a monophyletic taxonomic usage could be employed to avoid relational confusion. Under this recommendation, "shark" could be defined as the last common ancestor of *Chlamydoselachus* and *Carcharodon*, and all of its descendants, though that would exclude most fossil taxa (including *S. striatus*). As unpalatable as "ctenacanthid chondrichthyan" might be, it is the truer statement of taxonomic relationship.

Synthesis

The provenience of EH23 and the location of the northeastern Tennessee cladodont remain unknown, though the Greenbrier Limestone in Virginia and Newman Limestone in Tennessee, respectively, are likely sources. These are the thickest and most fossiliferous units in the area representing a middle stage in a clastic-carbonate-clastic sequence (Ettensohn et al., 2022) before final marine closure in the later Carboniferous. These rocks preserve some of the latest records of the Rheic Ocean in advance of the Alleghenian Orogeny and subsequent uplift and deformation of Paleozoic strata in the southern Appalachians. Later rocks of the region are mostly freshwater and semi-terrestrial deposits, rich in coal and known for their many plant fossils (Butts, 1940).

The presence of *S. striatus* in these deposits, though not unexpected, provides a glimpse into a Paleozoic ecosystem in a region that has been little studied. With individual teeth reaching 6 cm in length (Duffin & Ginter, 2006), *S. striatus* was likely one of the largest predators of the Early Carboniferous seas but appears to have gone extinct before the Bashkirian Stage (Late Carboniferous). The genus, however, appears to survive into the Permian (Hodnett et al., 2012; Ivanov et al., 2020; Feichtinger et al., 2021). Though its exact geological provenience in the study area remains unknown, the reported locality for EH23 indicates that it is from a late Viséan-Serpukhovian unit in southwestern Virginia, which also corresponds with the stratigraphically contiguous northeastern Tennessee "*Cladodus*". The Lower Carboniferous system in southwestern Virginia and northeastern Tennessee provides a rich assemblage of plant, animal, and ichnofossil remains that warrant further scientific attention.

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