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First occurrence of the urocordylid *Ctenerpeton remex* from the Mazon Creek Lagerstätte, Illinois, USA

Blue M. Byrnes, John R. Bolt †, and Arjan Mann*
Negaunee Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, U.S.A.; arjanm@fieldmuseum.org; bluebyrnes@gmail.com

Abstract: Despite being one of the most complete records of a Paleozoic ecosystem, tetrapod fossils at the Mazon Creek Lagerstätte, in Illinois, USA, remain relatively rare compared to other contemporary late Carboniferous localities, making new additions to this fauna particularly important. Here we report a new concretion from Mazon Creek that preserves an impression of a series of articulated caudal vertebrae of the early tetrapod *Ctenerpeton remex*. It can be differentiated from *Ptyonius* and other nectrideans by the characteristics of its neural and haemal spines and arches, most notably the anterior and posterior projections on the haemal arches, the accessory zygapophyses on the neural arch, and the size and shape of the spines compared to known specimens of other urocordylids and nectrideans. The addition of *Ctenerpeton remex* to the Mazon Creek tetrapod assemblage increases the known diversity of nectrideans in this fauna and aids in our understanding of the different environments inhabited by urocordylids in the late Carboniferous.

INTRODUCTION

The Carboniferous, late Pennsylvanian, Moscovian-age (309–307 Ma), Mazon Creek Lagerstätte of northern Illinois contains one of the best-known records of a late Paleozoic ecosystem (Shabica and Hay 1997; Clements et al., 2018). The tetrapod fauna from Mazon Creek has been recently revisited in a series of papers detailing new discoveries, most of which belong to the clade of highly fossorial recumbirostran 'microsaurs' (Mann and Maddin 2019; Mann et al. 2019a, 2019b; Mann and Gee 2019; Mann et al. 2021; Mann et al. 2022). This recent research has challenged long standing beliefs that the Mazon Creek Lagerstätte is lower in tetrapod diversity than contemporary sites such as Linton, Ohio (Moodie, 1912; Gregory, 1998; Shabica and Hay 1997). Despite these new works, there are still many aspects of the tetrapod fauna that require further revision, including the diversity of temnospondyls, aistopods, and nectrideans from the site. Tetrapods from Mazon Creek are uniquely found in siderite concretions, broken apart though freeze-thaw cycles (natural or artificial), into part and counterpart, usually down the midline of the animal, revealing natural molds of tetrapod remains inside (Shabica and Hay 1997).

Here we report a new tetrapod fossil from Mazon Creek that was collected from an unknown spoil pit locality, likely Pit 11 (Clements et al. 2019), by Helen and Ted Piecko. The specimen, FMNH PR 1799, preserves a partial articulated tail of a large nectridean that most closely resembles the caudal vertebrae of those found in *Ctenerpeton remex*, a nectridean tetrapod known previously only from Linton and Five Points, Ohio. At Linton, *Ctenerpeton* is a relatively rare member of the vertebrate fauna, known from only a handful of specimens, with more complete fossils only coming to light in recent years (Hook and Baird 1986). The first fully articulated remains of *Ctenerpeton*, including the skull, are from Five Points, Ohio, but these have yet to be described in detail (Hook and Baird 1993). Previously, the only record of a nectridean from Mazon Creek was *Ptyonius marshii*, known from two relatively small individuals (FMNH PR 1353, USNM PAL 18125). FMNH PR 1799, although limited in the preserved remains, adds an important rare tetrapod to the assemblage at Mazon Creek.

MATERIAL & METHODS

Photographs were taken using a Canon EOS R10 camera with a Canon 35 lens. All figures were assembled and formatted in Clip Studio Paint Version 1.132. We compared FMNH PR 1799 to fossils of *Ctenerpeton* and other Permo-Carboniferous nectrideans at the Carnegie Museum of Natural History (CM), Pittsburgh, the American Museum of Natural History (AMNH), New York, the Field Museum of Natural History (FMNH PR), and

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the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM PAL).

SYSTEMATIC PALEONTOLOGY

TETRAPODOMORPHA Ahlberg, 1991

NECTRIDEA Miall, 1875

UROCORDYLIDAE Lydekker in Nicholson and Lydekker, 1889

Ctenerpeton Cope, 1897

Ctenerpeton remex (Cope, 1868)

Referred Material: FMNH PR 1799, a partially articulated caudal series, containing 21 complete and 2 partial vertebrae, contained in part and counterpart in a siderite concretion (Fig. 1).

Locality and Horizon: Unknown spoil pile locality (likely Pit 11 based on other collections by the collectors), Mazon Creek, Will and Grundy County, Illinois, Francis Creek Shale above the Morris (no. 2) Coal, Carbondale Formation, Pennsylvanian (Moscovian). Collected by Helen and Ted Piecko.

Figure 1. Specimens of *Ctenerpeton remex*. A, FMNH PR 1799, part and counterpart concretion from Mazon Creek, Illinois, USA, showing the impressions of a partial tail of *Ctenerpeton*. B, CM 34912, a comparative postcranial skeleton including tail of *Ctenerpeton* from Five Points, Ohio, that shows similar anatomy.

DESCRIPTION

Comparative Osteology of FMNH PR 1799: This specimen, preserved in a siderite nodule, consists of a natural mold of 21 complete and two partial caudal vertebrae in part and counterpart. The anatomy preserved in FMNH PR 1799 has notable overlap with the holotype of *Ctenerpeton remex*, AMNH 6907, which consists of 23 caudal vertebrae. The following description is based on epoxy casts (Fig. 2) that were made from latex peels of FMNH PR 1799.

The neural and haemal spines are strikingly symmetrical, both being slender and elongate fans, and are characteristic of caudals belonging to nectrideans (Bossy 1979). The distal ends of adjacent spines never touch. Both neural and haemal spines are grooved distally with the grooves extending into fine serrations at the margin. In lateral aspect, the haemal spines have two parallel emarginations on either side of a median ridge extending distally, whereas the neural spine frequently has a single median groove. This condition is also observed in the holotype of *Ctenerpeton remex*, AMNH 6907.

The neural arch possesses well developed pre- and post-zygapophyses which are oriented horizontally. Three pairs of horizontal accessory apophyses between neural arches, characteristic of Urocordylinae (Carroll et al. 1998), are present (Fig. 2).

The articular regions of the haemal arch consist of thin, semi-circular laminae, that occasionally bear small finger-like projections on both anterior and posterior ends (Figs. 2, 3A). The articular regions occasionally abut and do not seem to consistently possess the three finger-like projections that typically are described as articulating with the adjacent haemal arches (Bossy 1976).

DISCUSSION

The size and shape of the neural and haemal fans on FMNH PR 1799 clearly demonstrate that this is not referable to *Sauropleura*, *Pytonius*, *Urocordylus* or any other nectridean such as diplocaulids (Figs. 2, 3). In *Sauropleura*, both the neural and haemal spines are short and broad, approaching equilateral triangles in shape (Bossy 1976). *Pytonius* possess haemal spines which are broader distally than their corresponding neural spines and a thickened haemal arch (Fig. 3B). *Urocordylus* also has a shorter, broader, haemal spine and a haemal arch lacking the articulating projections found in both *Ptyonius* and *Ctenerpeton* (Bossy 1976; Carroll et al. 1998).

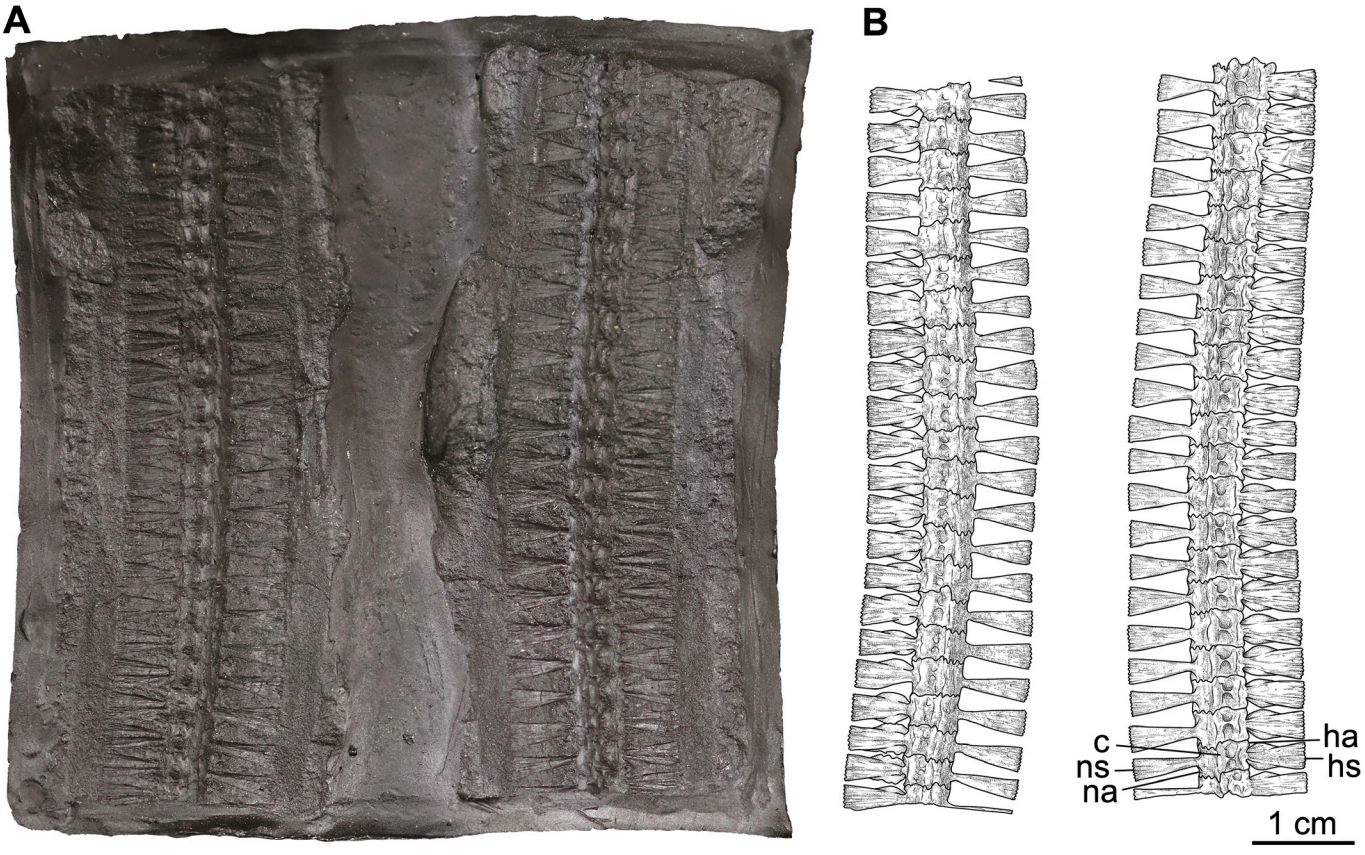

Figure 2. *Ctenerpeton remex* from Mazon Creek, Illinois. A, FMNH PR 1799, epoxy cast of the partial caudal vertebral column showing the positive relief. B, Interpretive illustration of part and counterpart based on Figure 2A. Abbreviations: c, centrum; ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine.

Bossy (1976) established numerous criteria by which a series of articulated caudal vertebrae of *Ctenerpeton* may be placed into their proper position in the caudal sequence. Using these, we determined that the new fossil preserves caudal vertebrae 5–25. Originally, a much more complete specimen may have been preserved. The nodule containing FMNH PR 1799 is incomplete at both ends and was probably broken upon exposure or during mining operations at the site of the specimen's discovery.

In recent reviews of the Mazon Creek tetrapod assemblage (Shabica and Hay 1997; Clements et al. 2019; Mann 2020), only one nectridean taxon, *Pytonius marshii* was recorded as present. The specimen upon which this occurrence is based (USNM PAL 18125) was originally identified as *Sauropleura* by Gregory (1950), but was reidentified as *Pytonius* by Bossy (1976). Since then, an additional specimen of *Ptyonius* (FMNH PR 1353) was figured by Stephen J. Godfrey in the tetrapod chapter of the Richardson's Guide to The Fossil Fauna of Mazon Creek (Shabica and Hay 1997). Unfortunately, this second specimen has never been described formally despite its exceptional preservation of soft tissues and diminutive size. This specimen will be highly important to include in our planned anatomical revision of the genus *Ptyonius* and for understanding patterns of ontogeny in this taxon.

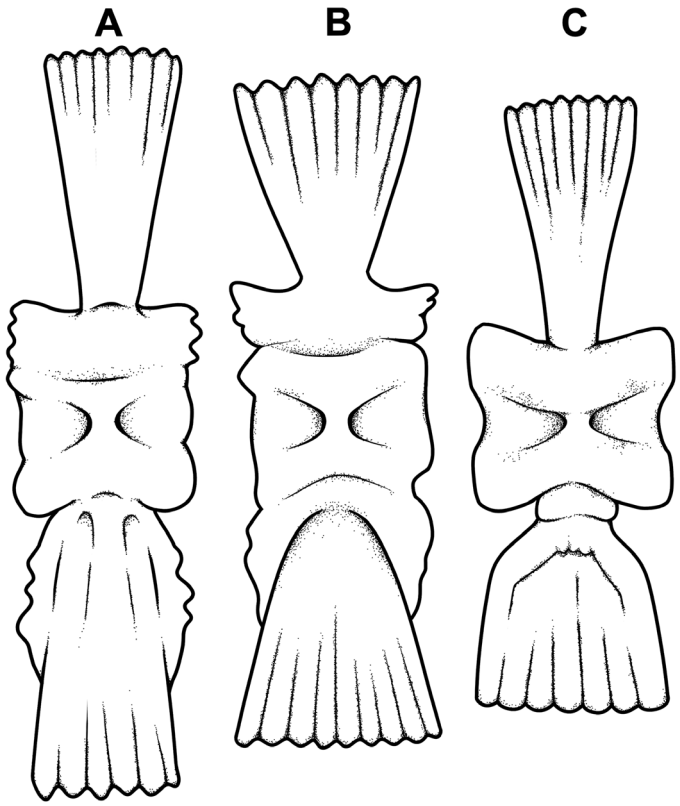

Figure 3. Comparative caudal vertebral anatomy of Urocordylinae. Not to scale. A, *Ctenerpeton remex*. B, *Ptyonius marshii*. C, *Urocordylus wandesfordii*.

In the present study, we have reported the first record of the nectridean *Ctenerpeton remex* from Mazon Creek, adding to the diversity of its tetrapod assemblage and bringing this locality somewhat closer in line with the diversity of tetrapods known from similarly aged coal measure localities (e.g., Linton, Ohio). This new record also extends the paleogeographic and paleoenvironmental range which *Ctenerpeton* inhabited.

Nectrideans can be quite diverse and abundant across other Carboniferous 'coal measure' localities, often comprising the majority of tetrapod fossils found at these localities (Hook and Baird 1986). Notably, nectrideans are absent from both Joggins and Florence, Nova Scotia, Canada. However, this may be a taphonomic artifact related to the unique preservation of tetrapods in lycopsid tree stumps at these localities, and may not reflect their true absence in these ecosystems. Of the localities where nectrideans are found, they are usually preserved in cannel coals (e.g., Nýřany, Czech Republic, Linton and Five Points, Ohio, USA), where they are both abundant and diverse in their clade representation (e.g., keraterpetontids, scincosaurids, urocordylids). Cannel coal-type preservation often is representative of paleoenvironments including freshwater oxbow lakes or abandoned channels, that were infilled with sapropelic peat over time (Hook and Ferm, 1985). It is possible that the rarity of nectrideans at Mazon Creek reflects environmental preferences by these tetrapods and that the estuarine, brackish water conditions in the paleoenvironment of Mazon Creek was not ideal for nectrideans that preferred more inland freshwater environments (Hook and Baird 1986; Schiffbauer et al. 2025). At present, there are no records of any other nectridean clades beyond the family Urocordylidae present at Mazon Creek, and these are only represented by the two genera *Ctenerepton* and *Ptyonius*. However, continued collection at Mazon Creek may reveal further diversity.

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research notes of the late Dr. John R. Bolt, former Curator of Fossil Amphibians and Reptiles at the Field Museum of Natural History, who first recognized the specimen as belonging to *Ctenerpeton*. John R. Bolt is included here as an author to honor his memory and many contributions to the field of early tetrapod paleontology.

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