Journal of Paleontology, 97(1), 2023, p. 167–171 Copyright © The Author(s), 2022. Published by Cambridge University Press on behalf of The

Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

0022-3360/23/1937-2337 doi: 10.1017/jpa.2022.84



# **Eurypterids from the Price Formation of Virginia: First Eurypterids from the Mississippian of North America**

Roy E. Plotnick<sup>1\*</sup> o and James C. Lamsdell<sup>2\*</sup> o

**Abstract.**—A new hibbertopterid eurypterid, *Cyrtoctenus bambachi* n. sp., is described from the Early Mississippian (Tournaisian) Price Formation of western Virginia. The same unit yields an unidentifiable stylonurine eurypterid. These are the first eurypterids documented from the Mississippian of North America, and only the fourth locality of this age anywhere in the world to yield eurypterids.

UUID: http://zoobank.org/5c84d3a2-ea5a-402c-970d-9b0d867f52c7

### Introduction

Eurypterids are rare components of Mississippian faunal assemblages. Only three families are known, although they belong to both suborders, the Eurypterina and the Stylonurina (Table 1). These same higher taxa persist until the final extinction of the eurypterids during the Permian, with overall diversity remaining low (Lamsdell et al., 2010; Lamsdell and Selden, 2017). In late Paleozoic strata, eurypterids are found only in freshwater environments (Lamsdell and Selden, 2017).

The geographic range of Mississippian eurypterids is also limited (Tetlie, 2007). More than half of the Mississippian eurypterids come from Visean and Serpukhovian units in Scotland and were described in detail by Charles Waterston (Waterston, 1957, 1968; Størmer and Waterston, 1968). Additional early Carboniferous eurypterid localities in Scotland were mentioned but not described by Smithson et al. (2012). Outside of Scotland, only *Cyrtoctenus wittebergensis* Waterston, Oelofsen, and Oosthuizen, 1985, from the Tournaisian of South Africa is well known. Here, we describe the first Mississippian eurypterids from North America and only the fourth eurypterid occurrence known from the Tournaisian.

#### **Geological setting**

The Price Formation is a Lower Mississippian unit exposed in a narrow outcrop belt in the Appalachians from Virginia northeast into Pennsylvania (Kammer and Bjerstedt, 1986; Bjerstedt and Kammer, 1988; Nolde, 1994). It is interpreted as a southwest-prograding deltaic complex, comprising a complex of marine, delta front, and coastal alluvial facies, including coal-producing

\*Corresponding author.

swamp deposits (Kreisa and Bambach, 1973; Bjerstedt and Kammer, 1988). In Virginia, the upper part of the Price, which contains the deltaic sequence, is dated as Kinderhookian to lower Osagean (Kammer and Bjerstedt, 1986; Bjerstedt and Kammer, 1988; Gensel, 1988; Gensel and Pigg, 2010) or solely Osagean (Nolde, 1994), which corresponds to Tournaisian. Two localities in the Virginia portion of the outcrop belt (Brush Mountain-Little Walker Mountain outcrop belt; Bjerstedt and Kammer, 1998, fig. 2) have yielded specimens of eurypterids from shales.

Locality 1: Coal Bank Hollow.—About 100 m of the Price Formation is exposed along U.S. 460, between Coal Bank Hollow Road and County Route 648 (Brown, 1983), Brush Mountain, 3.2 km north of Blacksburg, Montgomery County, Virginia (37.27571°N, 80.418900°W; WGS84). This is locality 11 of Kreisa and Bambach (1973). A detailed section of this site (with lithologies including sandstone, siltstone, claystone, and mudstone) was given by Brown (1983), who placed it in the upper part of the Price Formation. The fine-grained intervals are near the base of the section; a coal layer is near the top. Plants from the site listed by Jennings (1975) and Scheckler (1978, cited in Brown, 1983) consist of: Lepidodendropsis scobiniformes (Meek, 1880); L. vandergrachtii Jongmans, Gothan, and Darrah, 1937; Lepidophylloides sp., Protostigmaria eggertiana Jennings, 1975 (miscopied by Brown, 1983, as Protostigmaria essetiema); and Rhodea sp. The exact horizons yielding the eurypterid specimens are not known. The eurypterids from Coal Bank Hollow were briefly discussed in Briggs and Rolfe (1983), based on preliminary observations by Plotnick.

Locality 2: Pond Lick Hollow.—An exposure along County Route 674 (Pond Lick Hollow Road), west of Pulaski, Pulaski County, Virginia (37.054°N, 80.800°W; WGS84). This is



<sup>&</sup>lt;sup>1</sup>Department of Earth and Environmental Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, Illinois 60607, USA <plotnick@uic.edu>

<sup>&</sup>lt;sup>2</sup>Department of Geology & Geography, West Virginia University, 98 Beechurst Avenue, Brooks Hall, Morgantown, WV 26506, USA <james.lamsdell@mail.wvu.edu>

Clade	Species	Locality	Group/Formation	Age	References
Eurypterina					
Adelophthalmidae  Incertae sedis	Adelophthalmus irinae Shpinev, 2006	Siberia	Solomennyi Stan	Tournaisian	Shpinev, 2006
	Adelophthalmus? perornatus (Peach, 1882)	Scotland	Tyler Limestone, Glencartholm Volcanic Member	Visean	Waterston, 1957
	Unionopterus anastasiae Chernyshev, 1948	Kazakhetan	Karaganda	Mississippian	Chernyshev, 1948; Tetlie and
	Omonopierus anasiasiae Chernyshev, 1948	Kazakiistaii	Karaganua	wiississippiaii	Van Roy, 2006
Stylonurina					
Hibbertopteridae	Campylocephalus? salmi (Stur, 1877)	Czechia	Ostrava	Serpukhovian	
	Cyrtoctenus bambachi n. sp.	Virginia, USA	Price	Tournaisian	This paper
	Cyrtoctenus peachi Størmer and Waterston, 1968	Scotland	Calciferous Sandstone Series	Visean	Størmer and Waterston, 1968
	Cyrtoctenus wittebergensis Waterston, Oelofsen, and Oosthuizen, 1985	South Africa	Waaipoort	Tournaisian	Waterston et al., 1985
	Cyrtoctenus caledonicus (Salter, 1863)	Scotland	Calciferous Sandstone Series	Visean	Størmer and Waterston, 1968
	Hibbertopterus stevensoni (Ethridge, 1877)	Scotland	Cementstone Group	Visean	Waterston, 1968
	Hibbertopterus? hibernicus (Baily, 1870)	Ireland	Upper Old Red Sandstone	Tournaisian?	Braddy et al., 2022
	Hibbertopterus scouleri (Hibbert, 1836)	Scotland	East Kirkton Limestone	Visean	Waterston, 1957; Jeram and Selden, 1994
Mycteropidae	Mycterops? blairi Waterston, 1968	Scotland	Scottish Limestone Coal Group	Serpukhovian	Braddy et al., 2022
	Woodwardopterus scabrosus (Woodward, 1887)	Scotland	Tyler Limestone, Glencartholm Volcanic Member	Visean	Kjellesvig-Waering 1959; Waterston 1957, 1968

**Table 1.** Mississippian Eurypterids. Classification of Dunlop et al. (2020). Within genera, given in stratigraphic order (oldest to youngest). Note: *Hibbertopterus*(?) *hibernicus* from Kiltorcan, Ireland, may be latest Upper Devonian, rather than Tournaisian in age (Jarvis, 1990).

near to locality 6 of Kreisa and Bambach (1973) and is probably section C of Brown (1983, p. 54). This is also a coarsening upward sequence, with claystone at base and sandstone at the top. The specimens come from a gray/mottled white finegrained shale with abundant iron stains, with a diverse associated flora including *Triphyllopteris*, *Rhodeopteridium* (*Rhodea*), *Neuropteris*, *Lagenospermum*, and *Gnetopsis* (P. Gensel, personal communication, 1981). *Neuropteris antiqua* (Stur, 1877) and *Rhodeopteridium* sp. occur on the slab (P. Gensel, personal communication, 2018) that includes the eurypterid (Gensel, 1988). Again, the exact horizon of the eurypterid specimen is not known.

The two localities are non-marine strata, associated directly with the Price Formation delta complex. They are either delta plain (Facies 7 of Kreisa and Bambach, 1973) or swamp (Facies 8 of Kreisa and Bambach, 1973). Gensel (personal communication, 1981) favored either a levee or channel area of a delta plain deposit for the Pond Lick Hollow Road specimen.

# Materials and methods

Specimens from Coal Bank Hollow were collected by faculty and students at Virginia Polytechnic Institute and State University, including Chauncey G. Tillman, Frank Whitten, and David Goodman, and deposited in the collections of the Department of Geological Sciences. In 2021 they were transferred to the Virginia Museum of Natural History and given specimen numbers. The specimen from Pond Lick Hollow was collected by Patricia Gensel.

Specimens were photographed with a Canon PowerShot Pro Series S5 IS digital camera. Figure 1.1 was drawn with a camera lucida attached to a Wild M5 binocular microscope.

Repositories and institutional abbreviations.—Type and figured specimens examined in this study are deposited in the following

institutions: Virginia Museum of Natural History (VMNH), Martinsville, Virginia, USA, and the paleontology collections of the University of North Carolina (NCUPC), Chapel Hill, North Carolina, USA.

### Systematic paleontology

Order Eurypterida Burmeister, 1843 Suborder Stylonurina Diener, 1924 Family Hibbertopteridae Kjellesvig-Waering, 1959 Genus *Cyrtoctenus* Størmer and Waterston, 1968

Type species.—Cyrtoctenus peachi Størmer and Waterston, 1968.

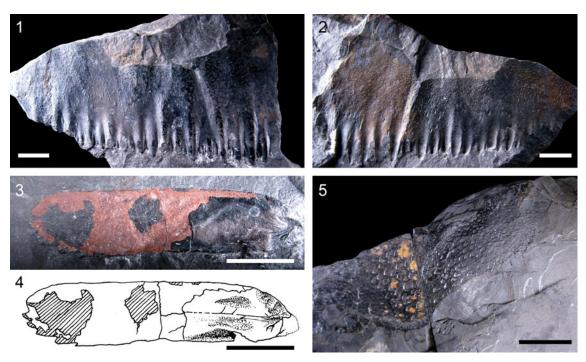
Cyrtoctenus bambachi new species Figure 1

*Holotype*.—VMNH 129168. Mississippian (Tournaisian), Price Formation, Coal Bank Hollow, near Blacksburg, Virginia, USA. Paratypes: VMNH 129166 and VMNH 129169.

Diagnosis.—Cyrtoctenus with cuticular ornamentation comprised of both acicular and lunate scales; prosomal appendage podomeres lacking distal crenulations; moveable fingers of prosomal appendage armature straight, expanding slightly distally, with rounded termination.

Occurrence.—Price Formation, Tournaisian (Kinderhookian–Osagean), at Coal Bank Hollow, Blacksburg, Virginia (37.27571°N, 80.418900°W), preserved in black shale.

Description.—Each type specimen is described individually below.



**Figure 1.** *Cyrtoctenus bambachi* n. sp. Price Formation, Lower Mississippian, Coal Bank Hollow, Virginia. (1, 2) VMNH 129166, opisthosomal tergite (paratype, part and counterpart). (3) Holotype: VMNH 129168, isolated free finger of prosomal appendage armature. (4) Camera lucida drawing of VMNH 129168. (5) VMNH 129169, cuticle and ornamentation (paratype). All scales 10 mm.

Holotype VMNH 129168.—Specimen comprises a moveable finger or blade with a length of 60 mm and a width of 10 mm proximally, expanding to 13 mm wide distally. The anterior (or dorsal) margin is straight, demarcated by a thickened ridge of imbricate scales. The posterior (or ventral margin) is slightly curved and is also ornamented with a ridge of imbricate scales. The distal termination of the finger is rounded, with four scales from the posterior margin projecting out to form blunt spines.

Paratype VMNH 129166.—Fragment of opisthosomal tergite in part and counterpart, preserved width 92 mm, preserved length 53 mm. No natural edge of the tergite is preserved except for the posterior margin, which is crenulated. Tergite strongly ornamented. Ornamentation grades from dense, small acicular scales anteriorly to larger, increasingly spread-out lunate scales posteriorly. The crenulation along the posterior margin is formed from a dense accumulation massively enlarged lunate scales that show significant relief, forming longitudinal ridges and furrows.

Paratype VMNH 129169.—Fragment of cuticle, most likely part of a prosomal appendage. The specimen has a length of 91 mm and is 21 mm wide proximally, expanding to 50 mm wide distally, with a recurved distal margin. The podomere is densely ornamented with acicular and semilunate scales that increase in size distally. An indentation running down the center of the podomere for 66 mm may represent a ventral groove.

*Etymology.*—Named for Richard K. Bambach, in honor of his many contributions to paleontology and the education of generations of paleontologists.

*Materials.*—Holotype VMNH 129168 and paratypes VMNH 129166 and VMNH 129169.

Remarks.—Braddy et al. (2022) synonymized the hibbertopterid genera Hibbertopterus, Dunsopterus, and Vernonopterus, but considered Cyrtoctenus to be distinct due to the presence of combs on the prosomal appendages. The Coal Bank Hollow material exhibits a tergite ornamentation more typical of Hibbertopterus (illustrated as Campylocephalus by Waterston, 1957) with dense acicular scales, and the enlarged acicular scales forming crenulations along the tergite posterior in VMNH 129166 specimens are also observed in specimens of Hibbertopterus formerly assigned to Dunsopterus (Waterston, 1968). The morphology of the podomere preserved at Coal Bank Hollow, VMNH 129169, closely matches podomeres of Hibbertopterus stevensoni (Etheridge, 1877) in ornamentation and overall morphology (Waterston, 1968). However, the moveable finger (VMNH 129168) is a clear indicator that the new species possessed combs and therefore is assignable to Cyrtoctenus (Størmer and Waterston, 1968; Waterston et al., 1985). The combination of traits in the new species further suggests that the genera Hibbertopterus and Cyrtoctenus may be synonyms (Jeram and Selden, 1994; Lamsdell et al., 2010; Lamsdell, 2013), although the current material is too sparse to warrant a full reassessment of the genera.

Despite being known from only a handful of fragmentary specimens, *Cyrtoctenus bambachi* n. sp. can be differentiated from other currently known *Cyrtoctenus* species based on the morphology of the moveable finger. The moveable fingers of *Cyrtoctenus peachi* and *Cyrtoctenus dewalqui* (Fraipont, 1889) are curved, narrow distally, and have pointed terminations (Størmer and Waterston, 1968), quite unlike those of *Cyrtoctenus bambachi* n. sp. *Cyrtoctenus wittebergensis* possesses moveable fingers that are straight, as in *Cyrtoctenus bambachi* n. sp., but narrow distally and terminate in a point. The moveable finger of *Cyrtoctenus* 



**Figure 2.** Stylonurina incertae sedis. Price Formation, Lower Mississippian, Pond Lick Hollow Road near Pulaski, Virginia. NCUPC 135A. Segments numbered 1–8. Scale 10 mm.

bambachi n. sp. is therefore unique among known *Cyrtoctenus* species in broadening distally and having a rounded termination. The lack of crenulations on the appendage podomere distal margins is also unique among *Cyrtoctenus* species.

# Stylonurina incertae sedis Figure 2

Occurrence.—Price Formation (Mississippian age) at Pond Lick Hollow Road (Co. Rt. 674), west of Pulaski, Virginia in gray shale with abundant plant fragments.

Description.—Seven, possibly eight, opisthosomal segments preserved with some relief. Anterior and posterior broken and incomplete. A large crack runs through the posterior of the specimen; the portion posterior to this can be removed. No

discernable ornamentation, trilobation, or division into preabdomen and postabdomen. Segment 1 is short. Indication of a marginal rim on some segments (left side segments 3–5; Fig. 2). Total length is 67 mm, maximum width is 29 mm.

Material.—NCUPC 135A.

Remarks.—The specimen lacks sufficient characters to confidently assign it to a taxon within the eurypterids. The lack of ornamentation on the segments, as well as no clear indication of a division into pre- and postabdomen, argues against inclusion within the Adelophthalmidae, the surviving clade of the Eurypterina (Lamsdell and Selden, 2017). The overall shape, smooth texture, and marginal rim resemble members of the Stylonurina, such as the Upper Devonian Stylonurella(?) beecheri Hall and Clarke, 1888 (Plotnick, 2022, fig. 8). Pending additional specimens, we place it as incertae sedis within the Stylonurina.

### **Discussion**

Although eurypterids are relatively common in both Late Devonian and Pennsylvanian terrestrial settings, they are by comparison extraordinarily rare in the Mississippian (Tetlie, 2007; Lamsdell and Selden, 2017). No members of the clade have been documented previously from North America. These specimens thus fill a key break in our understanding of the later history of this group.

Ward et al. (2006) suggested that terrestrial arthropods showed a chronological gap during the Visean equivalent to Romer's gap for vertebrates, which they attributed to low atmospheric oxygen levels. On the face of it, the record of Carboniferous eurypterids supports the existence of an arthropod gap. The forms reported here support the contention by Smithson et al. (2012) that the gap is an artifact of collection failure, with additional eurypterid material from this interval awaiting future discoveries.

### Acknowledgments

We are deeply thankful to R. Bambach for introducing us to the specimens from Coal Bank Hollow and allowing us to borrow them for an interminable amount of time. P. Gensel is similarly thanked for her loan of the specimen from Pond Lick Hollow and for her comments on its provenance and environment. J. Dunlop and an anonymous reviewer made useful comments which notably improved the manuscript.

# **Declaration of competing interests**

The authors declare none.

### References

Baily, W.H., 1870, On fossils obtained at Kiltorcan Quarry, Co. Kilkenny: Report of the Thirty-ninth Meeting of the British Association for the Advancement of Science, p. 73–75.

Bjerstedt, T.W., and Kammer, T.W., 1988, Genetic stratigraphy and depositional systems of the Upper Devonian–Lower Mississippian Price-Rockwell

- Deltaic Complex in the Central Appalachians, U.S.A.: Sedimentary Geology, v. 54, p. 265–301.
- Braddy, S.J., Lerner, A.J., and Lucas, S.G., 2022, A new species of the eurypterid *Hibbertopterus* from the Carboniferous of New Mexico, and a review of the Hibbertopteridae, Historical Biology. https://doi.org/10.1080/08912963.2022.2032690.
- Briggs, D.E.G., and Rolfe, W.D.I., 1983, A giant arthropod trackway from the Lower Mississippian of Pennsylvania: Journal of Paleontology, v. 57, p. 377–390.
- Brown, K.E., 1983., Stratigraphy and Deposition of the Price Formation Coals in Montgomery and Pulaski Counties, Virginia [M.S. thesis]: Blacksburg, VA, Virginia Polytechnic Institute and State University.
- Burmeister, H., 1843, Die Organisation der Trilobiten, aus ihren Lebenden Verwandten Entwickelt; nebst Systematischen Uebersicht aller Zeither Beschriben Arten: Berlin, G. Reimer, 148 p.
- Chernyshev, B.F., 1948, New representative of merostomata from the Lower Carboniferous: Kievski Gos., Universitet Insititutim T. G. Shevchenko, Geologicheskii Sbornik, v. 2, p. 119–130.
- Diener, C., 1924, Eurypterida, *in* Diener, C., ed., Fossilium Catalogus I: Animalia: Berlin, W. Junk, v. 25, p. 1–26.
- Dunlop, J.A., Penney, D., and Jekel, D., 2020, A summary list of fossil spiders and their relatives (https://wsc.nmbe.ch/resources/fossils/Fossils20.5.pdf), in Platnick, N.I., ed., The World Spider Catalog, version 23.5: Natural History Museum Bern. https://doi.org/10.24436/2.
- Etheridge, R., Jr., 1877, On the remains of a large Crustacean, probably indicative of a new species of *Eurypterus*, or allied Genus (*Eurypterus*? stevensoni), from the Lower Carboniferous Series (Cementstone Group) of Berwickshire: Quarterly Journal of the Geological Society of London, v. 33, p. 223–228.
- Fraipont, J., 1889, Euryptérides nouveaux du Dévonien supérieur de Belgique (Psammites du Condroz): Annales de la Société Géologique de Belgique, v. 17, p. 53–62.
- Gensel, P.G., 1988, On *Neuropteris brongniart* and *Cardiopteridium nathorst* from the early Carboniferous Price Formation, southwestern Virginia, U.S.A: Review of Palaeobotany and Palynology, v. 54, p. 105–119.
- Gensel, P.G., and Pigg, K.B., 2010, An arborescent lycopsid from the lower Carboniferous Price Formation, southwestern Virginia, USA and the problem of species delimitation: International Journal of Coal Geology, v. 83, p. 132–145.
- Hall, J., and Clarke, J.M., 1888, Descriptions of the trilobites and other crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung, and Catskill groups, Palæontology of New York, Volume 7: Albany, NY, Geological Survey of the State of New York, 236 p.
- Hibbert, S., 1836, On the fresh-water limestone of Burdiehouse in the neighbourhood of Edinburgh, belonging to the Carboniferous group of rocks. With supplementary notes on other fresh-water limestones: Transactions of the Royal Society of Edinburgh, v. 13, p. 169–292.
- Jarvis, E., 1990, New palynological data on the age of the Kiltorcan Flora of Co. Kilkenny, Ireland: Journal of Micropalaeontology, v. 9, p. 87–94.
- Jennings, J.R., 1975, Protostigmaria, a new plant organ from the lower Mississippian of Virginia: Palaeontology, v. 18, p. 19–24.
- Jeram, A.J., and Selden, P.A., 1994, Eurypterids from the Visean of East Kirkton, West-Lothian, Scotland: Transactions of the Royal Society of Edinburgh–Earth Sciences, v. 84, p. 301–308.
- Jongmans, W.J., Gothan, W., and Darrah, W.C., 1937, Beitrage zur Kenntnis der Flora der Pocono-Schichten aus Pennsylvanien und Virginia: Compte Rendus du Deuxième Congrés pour l'avancement des études de Stratigraphie Carbonifère, Heerlen, Netherlands, p. 423–444.
- Kammer, T.W., and Bjerstedt, T.W., 1986, Stratigraphic framework of the Price Formation (Upper Devonian–Lower Mississippian) in West Virginia: Southeastern Geology, v. 27, p. 13–33.
  Kjellesvig-Waering, E.N., 1959, A taxonomic review of some late Paleozoic
- Kjellesvig-Waering, E.N., 1959, A taxonomic review of some late Paleozoic Eurypterida: Journal of Paleontology, v. 33, p. 251–256.
- Kreisa, R.D., and Bambach, R.K., 1973, Environments of deposition of Price Formation (Lower Mississippian) in its type area, Southwestern Virginia: American Journal of Science, v. 273-A, p. 326–342.
- Lamsdell, J.C., 2013, Redescription of *Drepanopterus pentlandicus* Laurie, 1892, the earliest known mycteropoid (Chelicerata: Eurypterida) from the

- early Silurian (Llandovery) of the Pentland Hills, Scotland: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 103, p. 77–103.
- Lamsdell, J.C., and Selden, P.A., 2017, From success to persistence: identifying an evolutionary regime shift in the diverse Paleozoic aquatic arthropod group Eurypterida, driven by the Devonian biotic crisis: Evolution, v. 71, p. 95–110.
- Lamsdell, J.C., Braddy, S.J., and Tetlie, O.E., 2010, The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida): Journal of Systematic Palaeontology, v. 8, p. 49–61.
- Meek, F.B., 1880, Descriptions of new species of fossil plants from Allegheny County, VA: Philosophical Society of Washington Bulletin, v. 2, appendix 8, p. 26–44.
- Nolde, J.E., 1994, Devonian to Pennsylvanian stratigraphy and coal beds of the Appalachian plateaus province: geology and mineral resources of the southwest Virginia coalfield: Virginia Division of Mineral Resources Publication, v. 131, p. 1–85.
- Peach, B.N., 1882, Further researches among Crustacea and Arachnida: Transactions of the Royal Society of Edinburgh, v. 30, p. 511–529.
- Plotnick, R.E., 2022, Devonian eurypterids from Indiana and Pennsylvania: Contributions from the Museum of Paleontology, University of Michigan, v. 34, p. 5–16.
- Salter, J.W., 1863, The geology of eastern Berwickshire. Appendix—list of fossils—description of new cycadeous plant: Memoirs of the Geological Survey of Great Britain and of the Museum of Practical Geology, map 32, p. 58.
- Scheckler, S.E., 1978, Outcrops of the Price Formation (Lower Mississippian): Fieldtrip Guidebook, Paleobotany Section of the Botanical Society of America, Department of Biology, Virginia Polytechnical Institute and State University, Blacksburg, VA, 10 p.
- Shpinev, E.S., 2006, A new species of Adelophthalmus (Eurypterida) from the lower Carboniferous of the Krasnoyarsk region: Paleontological Journal, v. 40, p. 431–433.
- Smithson, T.R., Wood, S.P., Marshall, J.E.A., and Clack, J.A., 2012, Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap: Proceedings of the National Academy of Sciences, v. 109, p. 4532–4537.
- Størmer, L., and Waterston, C.D., 1968, Cyrtoctenus gen. nov., a large late Palaeozoic arthropod with pectinate appendages: Transactions of the Royal Society of Edinburgh, v. 68, p. 63–101.
- Stur, D., 1877, Beiträge zur Kenntnis der Flora der Vorwelt. Die Culm Flora. Part 1. Die Culm-flora des Marisch-Schlesischen Dachschiefer: Abhandlung der Königliche Geologische Reichanstalt, v. 8, p. 1–106.
- Tetlie, O.E., 2007, Distribution and dispersal history of Eurypterida (Chelicerata): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 252, p. 557–574.
- Tetlie, O.E., and Van Roy, P., 2006, A reappraisal of Eurypterus dumonti Stainier, 1917 and its position within the Adelophthalmidae Tollerton, 1989: Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, v. 76, p. 79–90.
- Ward, P., Labandeira, C., Laurin, M., and Berner, R.A., 2006, Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization: Proceedings of the National Academy of Sciences, v. 103, p. 16818–16822.
- Waterston, C.D., 1957, The Scottish Carboniferous Eurypterida: Transactions of the Royal Society of Edinburgh, v. 63, p. 265–288.
- Waterston, C.D., 1968, Further observations on the Scottish Carboniferous eurypterids: Transactions of the Royal Society of Edinburgh, v. 68, p. 1–20.
- Waterston, C., Oelofsen, B., and Oosthuizen, R., 1985, *Cyrtoctenus wittebergensis* sp. nov. (Chelicerata: Eurypterida), a large sweep-feeder from the Carboniferous of South Africa: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 76, p. 339–358.
- Woodward, H., 1887, On a new species of *Eurypterus* from the Lower Carboniferous shales of Glencartholm, Eskdale, Scotland: Geological Magazine, v. 4, p. 481–484.

Accepted: 2 September 2022