

## A NEW EURYPTERID LAGERSTÄTTE FROM THE UPPER SILURIAN OF PENNSYLVANIA

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**ABSTRACT:** Eurypterids are generally rare in the fossil record, but occasionally occur in abundance. The genus *Eurypterus*, in particular, is well known from certain upper Silurian Lagerstätten of the northern Appalachian basin (New York and Ontario), but occurs far less frequently in the central and southern Appalachian basin (Pennsylvania, Maryland, and West Virginia, respectively). The recent discovery of an exceptionally preserved mass assemblage of *Eurypterus* in the upper Tonoloway Formation (upper Ludlow–Prídoli) of Pennsylvania provides new information on the behavior and life habitat of the genus in this region. Eurypterids at this locality are found in thinly laminated, calcareous shale deposited within the lower intertidal to shallow subtidal zone of a coastal mudflat or sabkha. Rare associated fauna of limited diversity, and evaporitic and desiccation features in associated beds, suggest a stressed environment with variable salinity and possible hypoxic conditions. Most eurypterids are disarticulated and fragmentary, but several fully articulated, exceptionally preserved specimens are present. Exoskeletal features and taphonomic indices values indicate a molt rather than death assemblage, and the presence of arthropod trackways suggests that *Eurypterus* sp. may have molted *en masse* in the vicinity of the burial site. Sequence stratigraphic interpretation of the site suggests that preservation of eurypterid remains is the result of occupation of ephemeral environmental (salinity/oxygen) conditions during a transgression. The occurrence of this new Lagerstätte within the upper Silurian succession of the central Appalachians, an interval which had heretofore yielded only rare, fragmentary remains, indicates that eurypterids were more prevalent in this region than previously thought.

### INTRODUCTION

Eurypterids are extinct, aquatic chelicerates considered to be the sister group to arachnids (Kamenz et al. 2011; Lamsdell 2013). First appearing in the Middle Ordovician period, initially in open marine settings, they reached peak diversity during the late Silurian before declining and becoming extinct at the end of the Permian, by which time they are found almost entirely within strata representing freshwater environments (Plotnick 1999; Lamsdell and Braddy 2010). Paleogeographically, eurypterids were widespread. They apparently originated, and were most prolific, on the paleocontinents of Laurentia and Baltica, before later expanding into Pangaea and adjacent areas (Tetlie 2007) (but see Lamsdell et al. 2013, for evidence of a possible Gondwana origin).

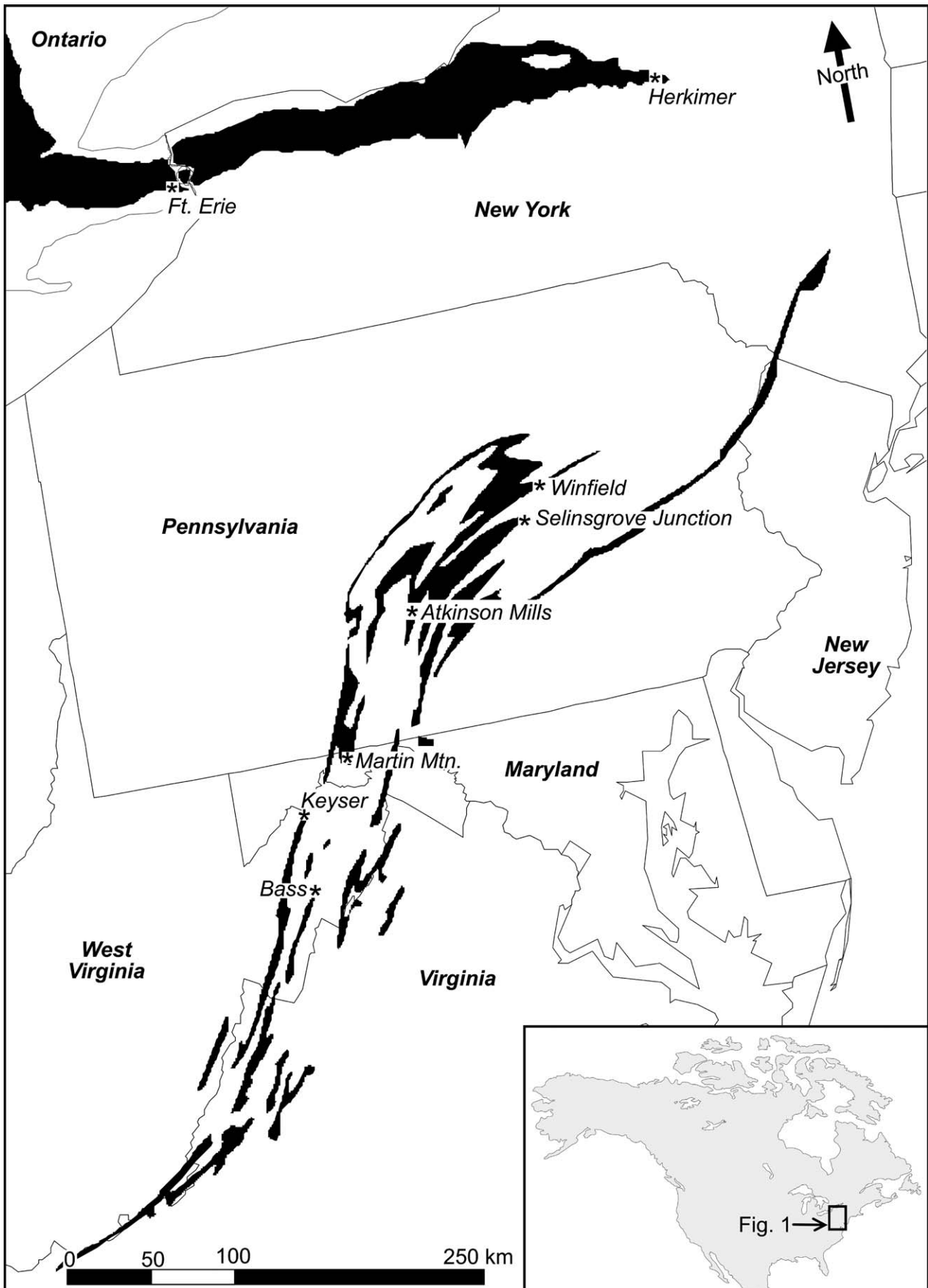
Despite their longevity and wide geographic dispersal, eurypterids are generally rare in the fossil record. Their fragile, non-biomineralized and lightly sclerotized cuticle, and frequent inhabitation of environments not conducive to preservation, e.g., shallow marginal marine or estuarine-type settings, limits the potential for eurypterid occurrences (Kluessendorf 1994). Even where conditions exist to allow for excellent preservation, most eurypterid fossils are disarticulated to some degree (Tetlie et al. 2008). Nevertheless, several eurypterid *Konservat-Lagerstätten* are known, such as within the upper Silurian Kokomo Limestone of Indiana and the Bertie Group of the northern Appalachian basin (New York and Ontario) (Kluessendorf 1994).

The dolomitic and chemically precipitated “waterlime” formations of the Bertie Group have produced the most profuse eurypterid assemblages in North America (Fig. 1), and are known not only for their extremely abundant and often exceptionally preserved eurypterids, but also for other

chelicerates including xiphosurans and early scorpions (Plotnick 1999, and references therein). Multiple eurypterid families and genera are found in the Bertie Group, but the genus *Eurypterus* is by far the most prevalent. For example, within the two most eurypterid-rich units of the Bertie group, the Fiddler's Green and Williamsville Formations, *Eurypterus* represents at least 85% of the eurypterid fauna (Kjellesvig-Waering and Heubusch 1962), and, consequently, is the most common taxon in many museum collections.

In the upper Silurian units of the central and southern Appalachian basin, however, eurypterid assemblages reported to date are less abundant and less diverse than those to the north (Plotnick 1999, and references therein). In these regions, a majority of documented upper Silurian localities occur in Maryland and West Virginia (Swartz 1923; Reger 1924; Tilton et al. 1927; Kjellesvig-Waering 1950; Leutze 1960; Kjellesvig-Waering and Leutze 1966), with only two poorly documented examples previously known from Pennsylvania (Schuchert 1903; S.J. Ciarca, Jr., personal communication 2012) (Fig. 1). Preservation also tends to be poor; specimens are preserved primarily as fragments or in an advanced state of disarticulation even when found in abundance (e.g., Kjellesvig-Waering and Leutze 1966). *Waeringopterus*, hughmilleriids and other pterygotoids dominate these eurypterid faunas (Kjellesvig-Waering 1950; Leutze 1960; Kjellesvig-Waering and Leutze 1966), whereas *Eurypterus* is strikingly rare: a single species (*E. flintstonensis*) is known from fragments at two localities (Swartz 1923; Tilton et al. 1927; Kjellesvig-Waering and Leutze 1966), and other *Eurypterus* remains are only known from isolated fragments (Schuchert 1903; Reger 1924; S.J. Ciarca, Jr., personal communication 2012).

There are two plausible explanations for the dearth of reported eurypterid assemblages from the upper Silurian central and southern



Appalachian basin: (1) depositional environments in this region were not conducive to eurypterid habitation and/or preservation, or (2) Pennsylvania, and to a lesser extent Maryland and West Virginia, are undersampled for eurypterids. The genetic similarities of late Silurian depositional environments in the northern Appalachian basin that produce eurypterid Lagerstätten (Clarke and Ruedemann 1912; Ciarca 1973; Kluessendorf 1994) to settings further south (e.g., Smosna et al. 1977) suggest the latter. In this case, further eurypterid assemblages may yet be prospected in this region (*sensu* Seilacher et al. 1985).

The recent discovery of a *Eurypterus* Lagerstätte from the upper Silurian Tonoloway Formation of Pennsylvania supports the premise that eurypterids are undersampled in the central Appalachian basin, and offers new insights into the paleoecology and taphonomy of this group. Using this abundant material, a taphonomic census was carried out (cf. Tetlie and Ciarca 2005), and we discuss possible biostratigraphic and taphonomic influences on this assemblage. Additionally, the integrated sedimentological and paleontological data allow for a paleoenvironmental and paleoecological reconstruction of the depositional environment of the upper Tonoloway Formation within a sequence stratigraphic framework. Within this stratigraphic context, we consider the implications for eurypterid preservation within marginal marine environments in the Appalachian basin.

#### GEOLOGICAL SETTING AND PALEOECOLOGY

The upper Silurian Tonoloway Formation (upper Ludlow–Přidolí; ~ 420 Ma) is the uppermost unit in the Salina Group (Cayugan Series) of the central and southern Appalachians and extends from northeastern Pennsylvania into Maryland, Virginia, and West Virginia. This formation lies on the eastern margin of a foreland basin. Enhanced tectonism in the mid-Silurian (Wenlock–early Ludlow), sometimes referred to as the Salinic orogeny, produced increased subsidence and the influx of the northwestwardly thinning Bloomsburg clastic wedge, which was up to 1500 m thick (Ettensohn and Brett 2002). By the late Silurian (late Ludlow–Přidolí), however, terrigenous input had been reduced and this, in addition to tectonic quiescence and limited subsidence, allowed for the formation of large areas of muddy carbonate deposition on the eastern and western margins of the basin (Dorobek and Read 1986; Bell and Smosna 1999).

Both the Appalachian and neighboring Michigan basins were highly evaporitic (Rickard 1969) due to a generally arid climate and restriction (or closure) of the basin to open oceanic water (Alling and Briggs 1961; Dennison and Head 1975; Smosna et al. 1977). In the Appalachian basin, these evaporite deposits are represented by the largely subsurface subunits of the Salina Group of western Pennsylvania, southwestern New York, and eastern Ohio (Alling and Briggs 1961). Southeast of this subsurface region, the exposed Wills Creek and Tonoloway Formations in the Appalachian fold-thrust belt record the marginal-marine and supratidal environments of the basin at this time (Carter 2007).

The restricted circulation of the Appalachian basin during the late Silurian also minimized tidal influence. Based on interpreted water-depth profiles, Smosna and Warshauer (1981) and Bell and Smosna (1999) calculated that the slope of the shoreface along the eastern margin of the Appalachian basin was very gentle (~ 0.0006), similar to that of the northern margin at that time (Belak 1980). They suggested that storm- or wind-driven currents were the main driver of small-scale, tide-like sea-

surface fluctuations, rather than strong diurnal or seasonal tides. A number of global eustatic events affected the Appalachian basin during the late Silurian (Johnson et al. 1998), including one event that occurred during deposition of the Tonoloway Formation. The end-Ludlow–Přidolí global transgression event resulted in up to 30 m of sea-level rise prior to a return to lowstand conditions later in the Přidolí. A later eustatic sea-level rise during the latest Přidolí–earliest Lochkovian (Dennison and Head 1975) reduced basin-wide salinity and evaporite deposition, and marked a return to continuous carbonate deposition in the eastern and northern regions of the basin (Inners 1981).

#### Stratigraphy and Depositional Environment

The Tonoloway Formation is exposed in central Pennsylvania, western Maryland, eastern West Virginia, and western Virginia (Heyman 1977). To the west, along the Appalachian basin axis in western West Virginia, Ohio, and western Pennsylvania, this formation is replaced by the upper subunits (D–G) of the subsurface Salina Group; to the north, in north-central Pennsylvania and New York, it is replaced by the Syracuse and Camillus Formations.

Across the Appalachian basin, the Tonoloway Formation has a conformable and gradational contact with the underlying Wills Creek Formation, differing from that unit through a reduction of shale beds (Cotter and Inners 1986), and it shares a disconformable contact with the overlying Keyser Formation that can be traced throughout the entire Appalachian basin (Woodward 1941). The Keyser Formation is a more fossiliferous, argillaceous, and nodular limestone unit compared to the Tonoloway Formation and is thought to represent a return to subtidal, marine conditions capable of supporting reefs (Makurath 1977; Laughrey 1999). However, despite the appearance of large, *in situ* reefs within the former, no evidence exists for similar offshore reef environments within the Tonoloway-equivalent units of western Pennsylvania (Alling and Briggs 1961; Smosna et al. 1977).

The Tonoloway Formation predominantly displays a peritidal–subtidal carbonate lithofacies succession and was deposited along a gentle ramp that sloped to the northwest toward the axis of the Appalachian basin (Smosna et al. 1977; Bell and Smosna 1999), although regional environmental variations and subdivisions exist. The Tonoloway Formation in Maryland and West Virginia has three informal subdivisions (Woodward 1941), whereas the Tonoloway Formation in central Pennsylvania has two members: an unnamed lower member correlative to most of the lower and middle units of West Virginia, and the overlying and much thinner Turbotville Member (Inners 1997); Pennsylvania is missing the slightly deeper water middle unit of West Virginia and Maryland (Bell and Smosna 1999).

In central Pennsylvania, the lower member is around 180 m thick and is characterized by abundant laminated to thinly bedded, evaporitic, argillaceous, and occasionally mud-cracked micritic dolostone and interbedded calcareous shale (Cotter and Inners 1986; Laughrey 1999). Other lithologies include evaporites, and minor skeletal wackestone, packstone, rudstone, and grainstone, depending on depositional depth. Repeated occurrences of stromatolites, microbial mat traces, “cryptogal” laminae, desiccation cracks and evaporite deposits, e.g., gypsum, halite, and calcite pseudomorphs (Ludlum 1959; Cotter and Inners 1986; Bell and Smosna 1999), indicate a restricted and arid lagoonal–tidal mudflat or sabkha-like environment with variable salinity that was regularly subjected to subaerial exposure.

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FIG. 1.—Regional map of the North American Appalachian basin. Shaded area represents known exposures of Silurian-age units; known *Eurypterus* localities, including study locality (Winfield, PA), are starred. In the Bertie Group of New York and Ontario, where *Eurypterus* is known from numerous localities, the Ft. Erie and Herkimer markers bound its approximate east–west range.

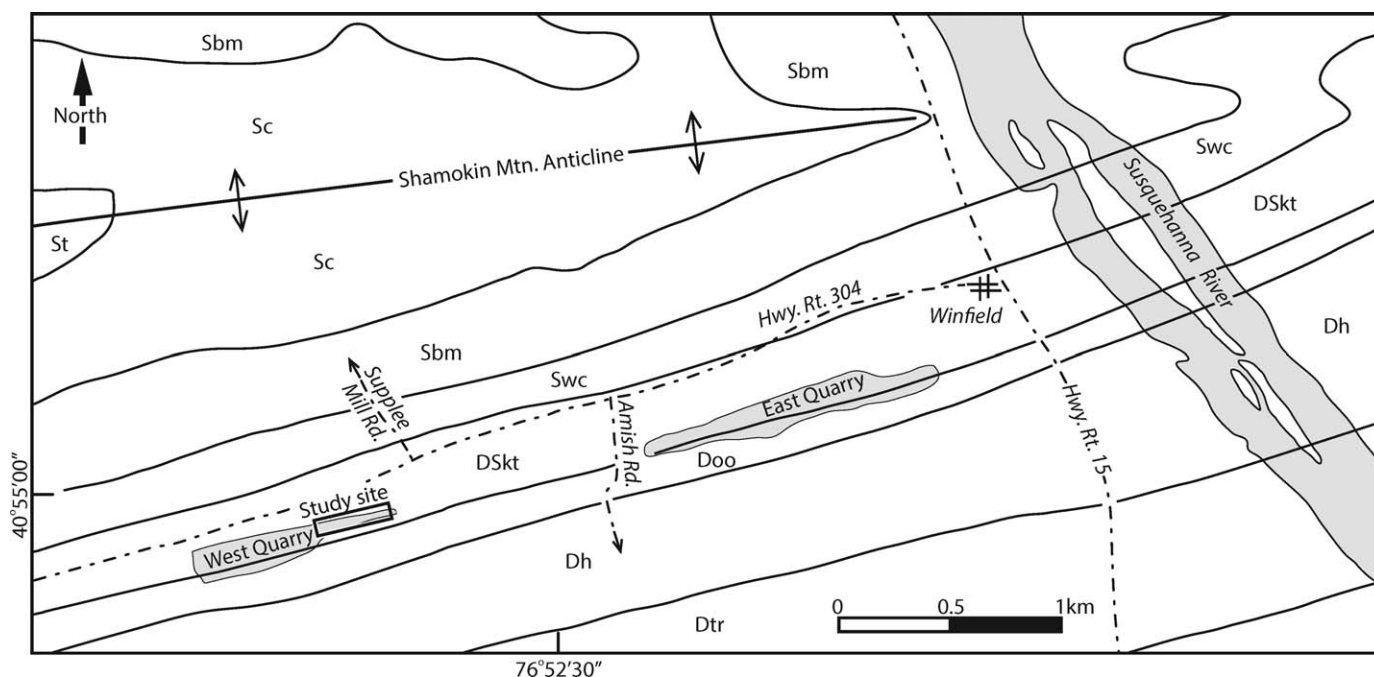


FIG. 2.—Map showing bedrock geology of the study area. Rectangle at east end of West Quarry marks the location of most eurypterid fossil collection during this study and the location of field photos shown in Figures 3–4, and measured stratigraphic section in Figure 5A. Abbreviations of Silurian–Devonian formations listed from oldest to youngest: Silurian—St = Tuscarora Formation, Sc = Clinton Group, Sbm = Mifflintown and Bloomsburg Formations, Swc = Wills Creek Formation; Silurian–Devonian—DSkt = Tonoloway and Keyser Formations; Devonian—Doo = Onondaga and Old Port Formations, Dh = Hamilton Group, Dtr = Trimmers Rock Formation. Adapted from Hoskins (1976).

The suprajacent Turbotville Member occupies the uppermost 9–15 m of the Tonoloway Formation in central Pennsylvania (Inners 1997) and conformably grades from the lower member. It is more fossiliferous, has a greater faunal diversity, and, for the most part, lacks the interbedded calcareous shale of the subjacent lower member. The Turbotville Member also displays less of the characteristic supratidal successions of the lower member and may represent high-intertidal to subtidal conditions consistent with an overall deepening-upward trend (Cotter and Inners 1986).

Cyclicality is prevalent throughout the Tonoloway Formation, including in Pennsylvania (Tourek 1970). For example, Cotter and Inners (1986) recorded 20+ subtidal–supratidal sabkha-type cycles of varying thickness through a ~ 150-m-thick exposure of the Tonoloway Formation at Allentown, Pennsylvania. Similar shallowing-upward cycles were also noted by Elick et al. (2009) from a Pennsylvania quarry roughly 70 miles to the east-northeast of Allentown.

**Fauna.**—Fossils are typically rare throughout the Tonoloway Formation and many intervals are barren. In those beds containing fossils, faunal diversity is generally low. In the landward inter- and supratidal facies associations that form the bulk of the formation, stromatolites and leperditicopid arthropods (*Leperditia*) dominate, while brachiopods including lingulids, gastropods, and fragments of bryozoans appear rarely (Warshauer and Smosna 1977; Inners 1997; Bell and Smosna 1999). Within the deeper subtidal deposits that occur throughout the formation, particularly to the southwest, a greater diversity of organisms exists, including bryozoans, various brachiopods, favositid and rugose corals, all of which appear to indicate an occasional return to normal marine (euhaline) conditions (Smosna and Warshauer 1981; Inners 1997; Bell and Smosna 1999).

#### Locality Description

The primary locality for this study is Winfield Quarry, a recently active and not yet reclaimed limestone quarry in Winfield, Pennsylvania

(40°53'55.04"N/76°53'26.13"W; Fig. 2). Quarrying activity has exposed units from the upper Silurian (Tonoloway Formation, uppermost lower member and Turbotville Member) through Lower Devonian (Old Port Formation, Ridgeley Member), dipping south-southeast at ~ 45° (Fig. 3A). Here, the uppermost 9 meters of the Tonoloway Formation are exposed, followed by the overlying Keyser Formation and Devonian units, which were described by Hess (2008) in a lithostratigraphic, chemostratigraphic, and paleontological study of the exposed outcrop interval.

Lithologically, the Tonoloway Formation at Winfield Quarry is predominantly thin- to medium-bedded micritic limestone, interbedded with thinly bedded and fissile calcareous shale and minor grainstone-to-packstone-to-rudstone units (Figs. 3B–F, 4A–F; see also Supplementary Data Fig. 1A–X, for additional details). Laminae, possibly of microbial origin, are the most common sedimentary structure (Fig. 4A; Supplementary Data Fig. 1C, I); desiccation cracks (Fig. 3C; Supplementary Data Fig. 1D–E), syneresis cracks (Fig. 4B), small (<1 cm) evaporitic? calcite-replaced vugs (Supplementary Data Fig. 1B), and shallow, linear, and symmetrical ripple marks (Fig. 4D; Supplementary Data Fig. 1J) are also present, but occur infrequently. Shallow scours occur throughout the section, but are more common in the lower shale units. The beds thicken upward in the section: shale and thin micrite beds are found toward the base of the exposure, and thicker micrite and grainstone beds are found near the top (Fig. 5A).

**Eurypterids.**—Eurypterids were first discovered at Winfield Quarry in 2008. They are found within two successive calcareous shale packages, either yellowish-weathering, dark chocolate brown or gray in color, that occur within a ~ 12-cm-thick interval of the Turbotville Member. The shale packages vary in thickness laterally across strike, but are typically ~ 6 cm thick and consist of two or three thin laminae of shale; the eurypterids occur on the uppermost laminae in both packages (EB1 and EB2 in Fig. 5A). The yellow coloration of some of the shale laminae is a result of iron weathering within the dolomitic component of the shale (Cotter and Inners 1986) and is distinct from the darker gray and thicker





FIG. 3.—Field photographs showing key stratigraphic and sedimentological features of the Winfield Quarry eurypterid fossil locality. Scales are as follows: A—vehicle for scale; B—person; C—hammer; D—camera lens cap; E—10-cm-long photo scale; F—no scale. A) Western part of Winfield Quarry showing uppermost Tonoloway Formation (Turbotville Mbr.) and overlying Keyser and Old Port Formations. Note dip slopes along right side of road where stratigraphic section (Fig. 5A) was measured and photos B–F and Fig. 4A–F were taken. E = area where nearly all eurypterid fossils were recovered. View toward the west. B) Uppermost Tonoloway Formation stratigraphy showing four key lithofacies associations from ~ 20 to 180 cm above base of measured section: D = micrite with desiccation cracks, T = micrite with thrombolites, L = laminated calcareous shale with eurypterid fossils, and P = interbedded limestone packstone, and subordinate grainstone/rudstone. View is toward the east. C) Desiccation cracks in micrite ~ 20 cm above base of measured section. D–E) Thrombolites ~ 40 cm above base of measured section. Note shaly laminae draping upon thrombolite in Part E. F) Thinly laminated calcareous shale 60–75 cm above base of measured section (continued in Fig. 4A).

sub- and suprajacent micrite beds. Eurypterids are found both *in situ* and in the talus at the base of the outcrop. Specimens found in float are easily traced back to their original stratum due to the steep dip-slope of the outcrop and limited exposure of stratigraphic intervals at any one point along strike.

Repeated collecting trips from 2008–2013, during which all visible eurypterid fossils (including fragments) were systematically collected, have yielded hundreds of well-preserved eurypterid specimens ( $N = 1756$ ). The layout of the quarry is such that nearly continuous bedding planes of the eurypterid-bearing horizons are exposed on a dip-slope for



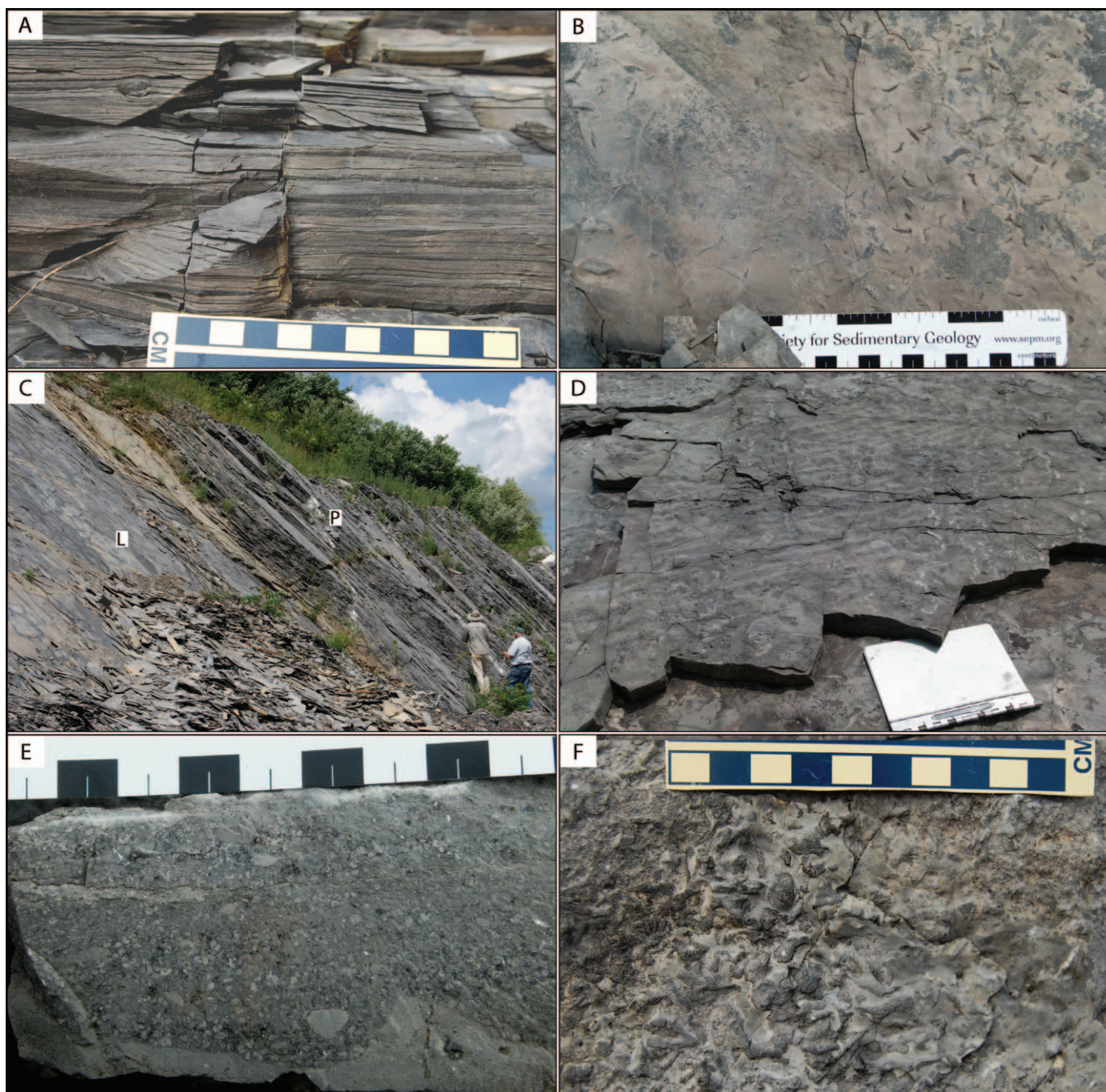


FIG. 4.—Field photographs showing key stratigraphic and sedimentological features of the Winfield Quarry eurypterid fossil locality. Note 10-cm-long photo scale in all photos except Part C (person) and Part D (clipboard). **A–B)** Thinly laminated calcareous shale 60–75 cm above base of measured section including close-up of laminae in Part A and syneresis cracks in Part B. **C)** Transition from calcareous shale (= L) to interbedded micrite, packstone, and minor grainstone (= P). Interval shown is ~ 70–720 cm above base of measured section. **D)** Low-amplitude, straight-crested ripples in wackestone/packstone ~ 575 cm above base of measured section. **E)** Poorly sorted rudstone with micritic intraclasts ~ 750 cm above base of measured section. **F)** Fragmented cladoporid? and leperditicopid fossils ~ 770 cm above base of measured section.

>700 m along strike. This feature permits exceptional access to the study interval and greatly increases the chances of finding eurypterids both in float and *in situ*.

The eurypterids are generally preserved as either impressions or compressed carbonized films with sediment infilling that display little relief. A small number of carbonized specimens can be freed from the

substrate and retain a slightly three-dimensional topology. Specimen completeness ranges from almost fully articulated examples with most appendages intact (rare), to disarticulated and isolated tergites, appendages, and fragments of cuticle (common); most specimens exhibit some degree of disarticulation (discussed further below) (Fig. 6–7). More fully articulated specimens tend to be isolated, whereas exoskeletal elements

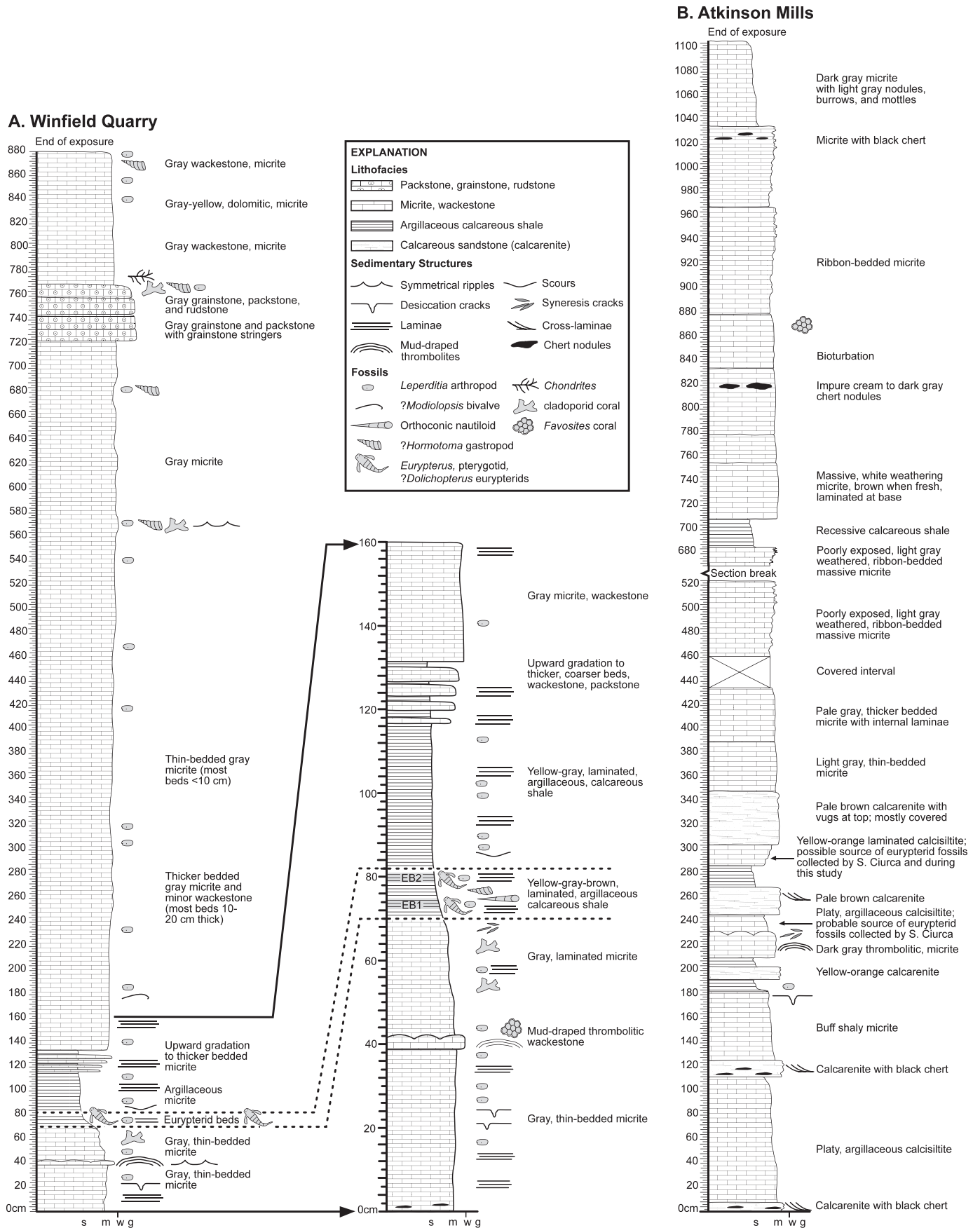
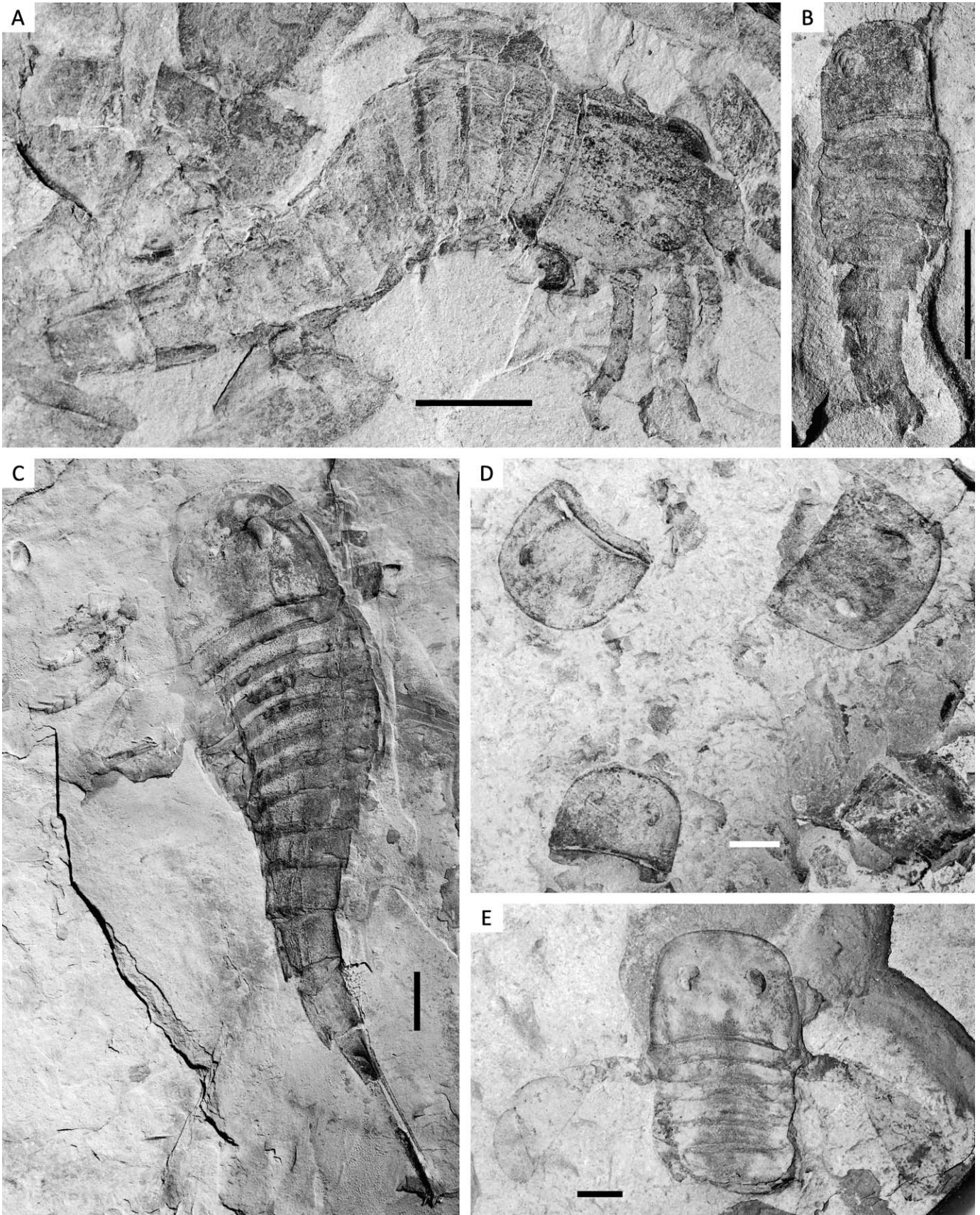


FIG. 5.—Lithological sections of study localities. A) Winfield Quarry, Pennsylvania. B) Atkinson Mills, Pennsylvania.







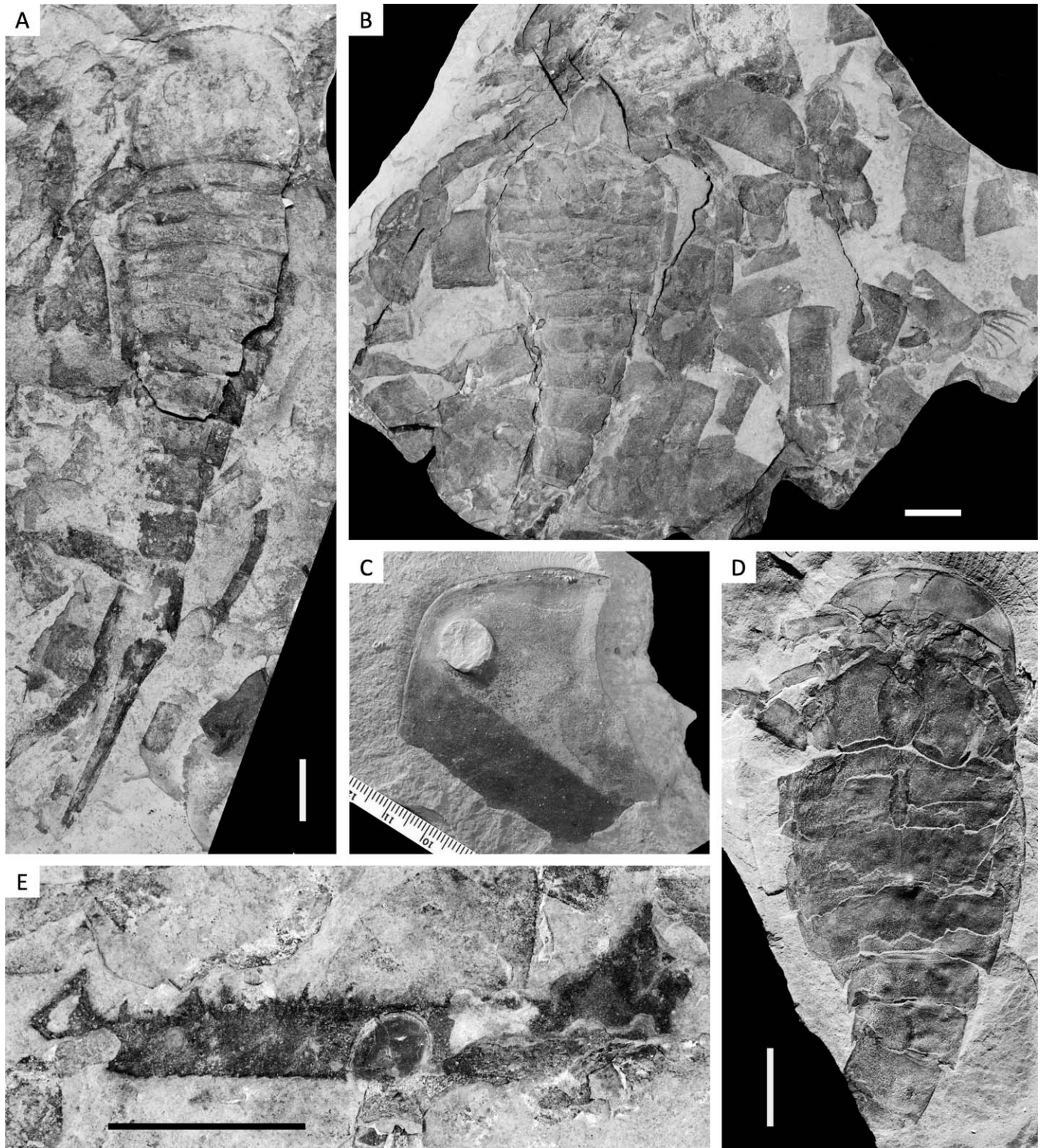


FIG. 7.—Eurypterids from the Tonoloway Formation, Winfield Quarry, Pennsylvania. Scale bars = 1 cm; ruler scale in cm. **A**) *Eurypterus* sp., nearly fully articulated (YPM 560633); **B**) *Eurypterus* sp., ventral-side up with appendages IV–VI visible, surrounded by disarticulated segment hash (YPM 560646). **C**) *Dolichopterus*, partial carapace (YPM 560637); **D**) *Eurypterus* sp., ventral-side up (YPM 560636); metastoma and genital appendage are visible. **E**) Isolated pterygotid finger (YPM 560635).

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FIG. 6.—*Eurypterus* sp., Tonoloway Formation, Winfield Quarry, Pennsylvania. Scale bars = 1 cm. **A**) Juvenile, preserved obliquely (YPM 560631). **B**) Juvenile (YPM 560634). **C**) Adult, appendages III–VI visible on left (YPM 560644). **D**) Isolated carapaces; the first tergite is attached to the two specimens on the left (YPM 560638, 560640, and 560641). **E**) Specimen with both swimming legs (appendage VI) attached (YPM 560642).



and fragments are often clustered together in fossil hashes (Fig. 7B). These hashes are similar in appearance to the eurypterid windrows of New York and Ontario, interpreted by Cieurca (2010) as current-accumulated eurypterid debris deposits. No eurypterid specimens found at Winfield Quarry contain features unequivocally indicative of a carcass such as preserved internal organs or muscle structures (cf. Braddy et al. 1995), but some specimens display features that have been attributed to ecdysis (see Tetlie et al. 2008, table 1, for features and references, and section 5.1 for disarticulation pattern). These include the frequent attachment of only the first abdominal segment with the carapace (Fig. 6D), separation of the dorsal prosomal unit from the ventral prosomal unit and remaining exoskeleton (Fig. 7B), and suture marks at the anterior end of the prosoma (Fig. 7D).

A detailed morphological and taxonomic treatment is not within the scope of this study, but preliminary comparison of the collected specimens to described taxa from the upper Silurian Appalachian basin suggests that all eurypterids found at Winfield Quarry, with the exception of two specimens (described below), are members of the genus *Eurypterus*, cf. *E. remipes*. *Eurypterus remipes* is known solely from the upper Silurian Fiddler's Green Formation (upper Pridoli) in New York and Ontario, a unit younger than the Tonoloway Formation. These specimens will be referred to as *Eurypterus* sp. herein. *Eurypterus* sp. is also very similar to *E. flintstonensis*, which is known from the Tonoloway Formation of Maryland (Swartz 1923) and West Virginia (Kjellesvig-Waering and Leutze 1966), and the contemporaneous Syracuse Formation of New York (Leutze 1961). However, *E. flintstonensis* may be a synonym of *E. remipes* or *E. lacustris* (Kjellesvig-Waering 1958)—themselves considered to be chronospecies (Tetlie et al. 2007), or slight variations of a single species—in which case the age range of *E. remipes* would be extended into older units. Evidently, a revision of this equivocal taxon is needed before any further assignments can be made.

Regarding the other eurypterid taxa, one specimen is a partial carapace of what appears to be a species within the family Dolichopteridae, possibly *Dolichopterus siluriceps* or *Clarkeipterus otisius* (J.C. Lamsdell, personal communication 2013) (referred to herein as ?*Dolichopterus*; Fig. 7C). Dolichopterids are common in the upper Silurian of Baltica and Laurentia (Plotnick 1999, and references therein), where they have been found in association with *Eurypterus* in New York (e.g., Clarke and Ruedemann 1912) and West Virginia (Leutze 1960, 1961), but this appears to be the first known occurrence of this family in the Tonoloway Formation. The second specimen is the fixed finger of a pterygotid chelicera, most likely from the genus *Acutiramus* (S.J. Cieurca, Jr., personal communication 2013) (Fig. 7E). *Acutiramus* and other pterygotids frequently co-occur with *Eurypterus* in the upper Silurian Bertie Group of New York and Ontario (Clarke and Ruedemann 1912; Plotnick 1999, and references therein) as well as in various units within the southern Appalachian basin (Leutze 1960; Kjellesvig-Waering and Leutze 1966). Their presence in the upper Silurian units of Pennsylvania is therefore expected, but this appears to be the first known occurrence of this taxon in the Tonoloway Formation.

**Associated Fauna.**—Non-eurypterid fossils are of limited diversity and generally sparse at the locality, with the exception of leperditicopids (*Leperditia*). *Leperditia* are extremely abundant on some shale layers, including the eurypterid-bearing units, and are found as isolated valves, dense hashes, or accumulations within shallow scours (Supplementary Data Fig. 1L–M, V). Valves are typically unabraded, predominantly convex-up, and range in size from 5–20 mm. Within these leperditicopid assemblages, molds of small, high-spired gastropods (<2 mm; ?*Hormotoma*) are also present, as are minute, fragmented bryozoans.

Other invertebrates present within the eurypterid-bearing layers are uncommon and are limited to small (<4 cm) tabulate corals (*Favosites*); a single unidentified bivalve preserved only as a dark periostracal film

(?*Modiolopsis*); highly compacted and fragmented orthoconic nautiloid cephalopods; and a possible juvenile pseudoniscine arthropod (?*Pseudoniscus*). In thicker argillaceous micrite beds below the eurypterid-bearing interval, *in situ* mud-draped thrombolites up to 30 cm long and ~ 8 cm high are present (Fig. 3D–E; Supplementary Data Fig. 1G), as are rare *Favosites*, abundant *Leperditia*, and gastropods. Within the thicker micritic wackestone and grainstone beds above the eurypterid-bearing units, the section becomes progressively more fossiliferous and disarticulated cladopod corals and *Leperditia* are abundant (Fig. 5A).

**Trace Fossils.**—Bioturbation and trace fossils are uncommon throughout the Tonoloway Formation. At Winfield Quarry, rare, *Chondrites*-like burrows only occur within the gray micrite beds ~ 7 m above the eurypterid horizons. Distinctive trace fossils, on the other hand, are common on one of the eurypterid-bearing shale horizons (EB1 on Fig. 5). The trace fossils vary from shallow, linear drag marks and recurrent pairs of curved grooves, to sporadic, chevron- or trifid-shaped impressions, some of which are directional in nature and appear to form symmetrical trackway pairs (Fig. 8). This combination of unique paired markings and their irregular distribution on the bedding surface appears to preclude them from being evaporitic in origin, i.e., early stage halite or gypsum molds, or current- or storm-derived sedimentary structures. Instead, the repeated fine, linear markings and shallow chevron-shaped tracks suggest an arthropod maker. Figure 8D shows some of the sharpest trace impressions. On this slab, several pairs of diametrically opposed chevron-shaped marks and a trifurcated drag mark occur alongside a longer, medial drag mark. These resemble chelicerate arthropod tracks such as the “simple tracks” and single chela tracks of either *Paramphibius*, an ichnogenus revised and ascribed by Caster (1938, fig. 1B; plate 1, fig. 3) to a Devonian xiphosuran similar to *Protolimulus*, or individual tracks within the putative eurypterid ichnogenus *Palmichmites* cf. *antarcticum* (Braddy and Milner 1998), further suggesting an arthropod tracemaker.

**Other Eurypterid-Producing Localities.**—To determine whether Winfield Quarry is a singular and areally restricted eurypterid-producing locality, or represents part of a larger regional assemblage, 13 additional localities with exposures of the Tonoloway Formation in the vicinity of Winfield, Pennsylvania were scouted (see Supplementary Data Table 1, for locality and reference details). Of these, the only localities known to have previously yielded eurypterids are Selinsgrove Junction and Atkinson Mills (Fig. 1). At Selinsgrove Junction, the uppermost Tonoloway and Keyser Formations are exposed for approximately one mile along an active railway on the east side of the Susquehanna River. A single *Eurypterus* fragment was found here by Schuchert (1903), but the exact location is unknown and the specimen is apparently lost. No additional material was found by us during recent fieldwork there.

The Atkinson Mills locality (40°27'13.58"N/77°49'33.72"W) is a small exposure of the Tonoloway Formation (upper Turbotville Member) through Keyser Formation that dips to the east-northeast on the south side of the intersection of US-22 E/US-522 N and T361 (Cookson Lane). Eurypterid specimens were collected here in the 1970s by Samuel J. Cieurca, Jr. from two horizons (S.J. Cieurca, Jr., personal communication 2012; Fig. 5B) and consist of several complete and partial carapaces of *Eurypterus* cf. *remipes* (M.B. Vrazo, personal observations 2012; Fig. 9A, B). These are now part of the Cieurca Collection at the Yale Peabody Museum of Natural History (YPM 215872–215894). During recent fieldwork at Atkinson Mills, the current authors obtained an isolated paddle and partial tergite from float (Fig. 9C, D). These specimens share the same lithology (calcisiltite) and distinctive color (yellowish-orange) as the lower Cieurca eurypterid horizon (~ 240 cm from base of outcrop) (Fig. 5B) and most likely originated there.



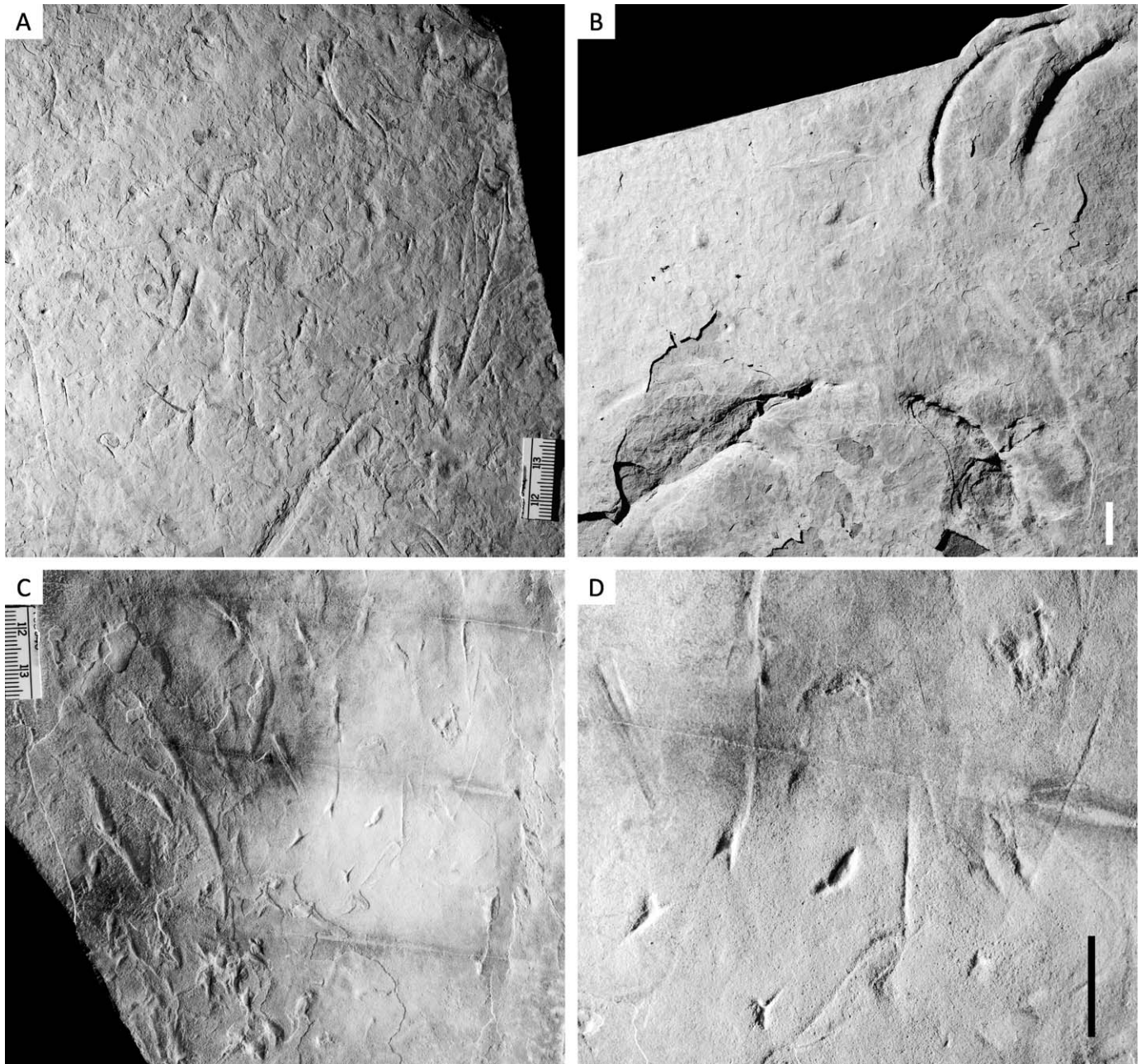


FIG. 8.—Trace fossils from the Tonoloway Formation, Winfield Quarry, Pennsylvania. Scale bars = 1 cm; ruler scale in cm. A) Trace ensemble (YPM 560645). B) Paired paddle-like traces (lower center) adjacent to deep paired drag marks (upper right) (YPM 560639). C) Trace ensemble (YPM 560643). D) Close-up of central portion of C; chevron-shaped (lower left) and trifurcated appendage (upper right) markings as well as a medial (telson?) drag mark (center right) are visible.

The eurypterid-bearing units at Atkinson Mills differ from those of Winfield Quarry in terms of lithology and color. Stratigraphically, however, the eurypterid-bearing beds occur within nearly identical vertical successions. At both localities, the eurypterid-horizons are preceded by a succession of beds containing chert, desiccation cracks, syneresis cracks, and thrombolites, respectively. Additionally, both exposures generally thicken upward and become predominantly micritic toward the overlying Keyser Formation. These stratigraphic similarities suggest that these are coeval units and that the chert, thrombolites, and desiccation features may be useful as marker beds for tracing the eurypterid horizons elsewhere.

#### POPULATION DISTRIBUTION AND TAPHONOMIC CENSUS

##### *Materials and Methods*

The size-frequency distribution of the eurypterid population at Winfield Quarry was determined using carapace length (a proxy for body length; Vrazo and Braddy 2011) measured digitally with ImageJ (Rasband 2011; accuracy =  $\pm 0.2$  mm [n = 10]). Because the prosoma is capable of being deformed and distorted both before and after burial (Tollerton 1989), significantly altered specimens were not measured; however, these are generally rare. Accurate recording of dorsal or ventral way-up orientation was not possible due to a large proportion of the material occurring as float.



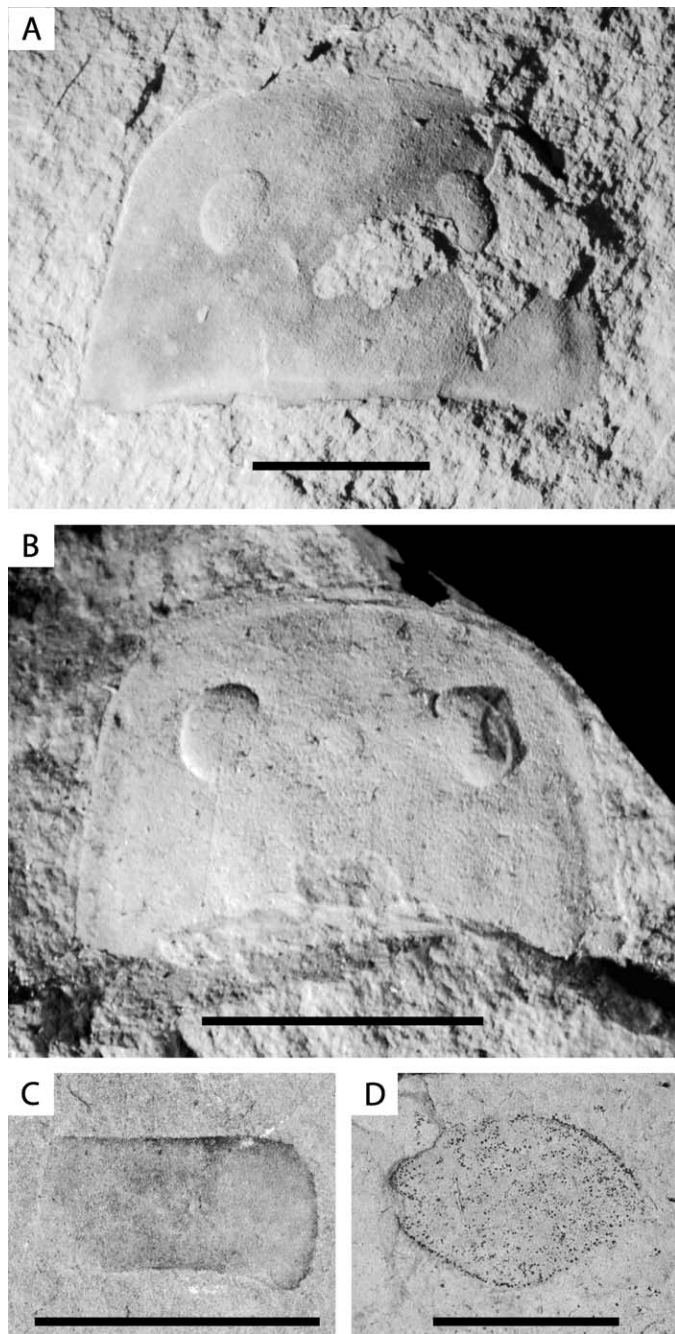


FIG. 9.—*Eurypterus* sp., Tonoloway Formation, Atkinson Mills, Pennsylvania. Scale bars = 1 cm. A) Isolated carapace (YPM 215893). B) Isolated carapace (YPM 215883). C) Partial sternite (YPM 560630). D) Paddle of swimming leg (appendage VI) (YPM 560632).

Although some specimens from Winfield Quarry display features consistent with molted remains (see above), such features are lacking on most specimens. In the absence of features diagnostic of either molts or carcasses, taphonomic indices can be used to quantitatively distinguish between a molt or death assemblage at the population level (Tetlie et al. 2008). To aid in determining whether the eurypterid fossils at Winfield Quarry represent a death or molt assemblage, a taphonomic census based on specimen completeness was carried out. All specimens examined as part of this census were found either *in situ* or in float directly beneath the only known eurypterid-bearing horizons at this locality. Eurypterid

specimen completeness was quantified using the Eurypterid Completeness Index (ECI), Carapace-Segment-Attachment-Index (CSAI), and Carapace-Appendage Attachment Index (CAAI) of Tetlie and Ciuca (2005). These indices, developed originally to perform a taphonomic census on the comprehensive Ciuca Collection at the Yale Peabody Museum, are based on the degree of disarticulation of individual specimens and can be averaged to evaluate the overall completeness of an assemblage. A similar taphonomic census was carried out by Vrazo and Braddy (2011, table 2) in an attempt to characterize the disarticulation pathway of assemblages of *E. remipes* and *E. lacustris* from the Fiddlers Green and Williamsville Formations, respectively, of the Bertie Group of New York and Ontario.

The ECI quantifies exoskeletal completeness by dividing a complete eurypterid into 26 individual elements (see Tetlie et al. 2008, p. 185, for specifics). Each complete element is coded as 1; partial elements are coded as 0.5, and isolated, unidentifiable fragments are coded as 0.1. For example, a fully articulated specimen would have a total score of 26, whereas an isolated telson would have a score of one. The CSAI and CAAS, on the other hand, are only based on the number of attached segments ( $\leq 12$ , ignoring the equivocal reduced 1st opisthosomal segment/microtergite [see Dunlop and Webster 1999]) or prosomal appendages ( $\leq 12$ ) attached to a carapace, respectively. Using either the CSAI or CAAS, a fully articulated specimen would have a total score of 12. A bias of the ECI is that mostly or fully articulated specimens will outweigh partial or fragmented specimens. All material from a given locality must therefore be collected and encoded to avoid collector bias. Limitations of this index are that exoskeletal fragments are often difficult to discern, especially when combined as a hash with other fragments, and such quantification can be time consuming and inaccurate. The CSAI and CAAI, on the other hand, ignore all fragmented and non-identifiable material, and may be more effective when collector bias is present, but will only be useful when articulated prosomas with attached segments or appendages are present.

The Ciuca Collection at the Yale Peabody Museum is considered qualitatively to lack significant collector bias (O.E. Tetlie, personal communication 2012); nevertheless, we decided to test for effects of potential collector bias. In comparing the sample size of individual localities against completeness index values (as a metric of potential bias), we found no significant correlation between the ECI, CSAI, and CAAI values calculated by Tetlie et al. (2008, table 6) for eight localities and their respective sample size (Pearson's;  $df = 6$ ,  $p > 0.05$ ). This indicates that the completeness index values obtained from these eight localities are independent of sample size, and can be utilized elsewhere as unbiased baseline indicators of death versus molt assemblages, and the depositional condition (i.e., high or low energy) of the latter (Tetlie et al. 2008).

### Results

Based on the measured length of 50 complete, or nearly complete, and undistorted carapaces, the eurypterids at Winfield Quarry represent a normally distributed ( $p > 0.05$ , one-tailed) population. The carapace lengths range in size from juvenile to fully grown adult ( $\sim 4$ –40 mm; mean: 20.15 mm; median: 22 mm; SD: 6.76) (Fig. 10), with most of specimens falling within what might be considered the young adult size class ( $\sim 22$ –28 mm). Vrazo and Braddy (2011) noted the subjective nature of previously assigned instar size classes, e.g., larvae, juvenile, adult, but a general growth stage of *Eurypterus* can be inferred not only from its overall size, but also the proportional size of swimming paddles compared to total length, and the gross morphology of its carapace. Juveniles have a quadrate carapace and rounded anterior margin, whereas adults have a more trapezoidal carapace and a flattened anterior margin. Additionally, the eyes become relatively smaller and move posteriorly on the carapace with growth (see Andrews et al. 1974, and Brower and Veinus 1978, for ontogenetic examples). The size-frequency distribution of the eurypterid specimens at Winfield Quarry is similar to the distributions found by



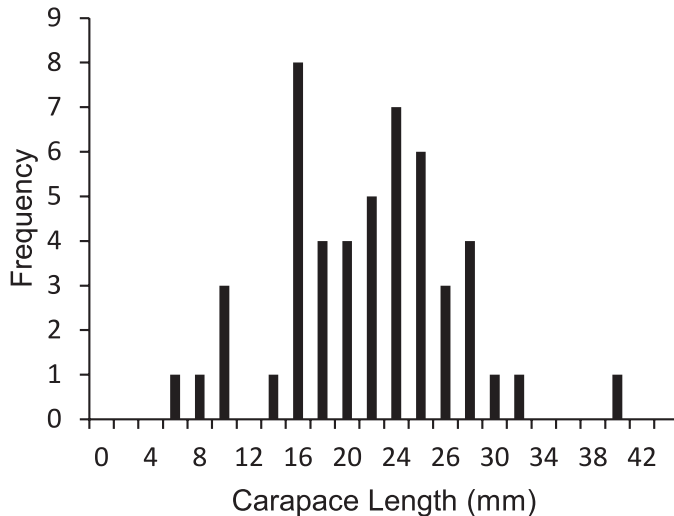


FIG. 10.—Size-frequency distribution of *Eurypterus* sp. carapaces from the Tonoloway Formation, Winfield Quarry, Pennsylvania ( $n = 50$ ).

others for late Silurian *Eurypterus* populations within the northern Appalachian basin (Andrews et al. 1974; Vrazo and Braddy 2011), with the caveat that the sample size of carapaces from Winfield Quarry is roughly one-third the sample size available to the latter two studies.

The results of the taphonomic census indicate that most of the specimens are disarticulated to some degree. Of the 59 exoskeletons with an attached prosoma, only 13 are fully articulated with the maximum number of tergites (12), and just over half of those (7) also had an attached whole or partial telson. The largest number of articulated prosomal appendages on any individual from the assemblage was 6.5 (out of 12). It should be noted, however, that only one chelicera was identified within the entire assemblage, and thus the presence/absence of chelicerae had virtually no influence on the census results discussed below.

The ECI value calculated for the *Eurypterus* sp. assemblage from Winfield Quarry is 1.06 ( $N = 1756$ ; range: 0.1–21.5). This value represents 4.07% of a fully articulated exoskeleton and the average percent of specimen completeness from this locality. This value is lower than all ECI values calculated by Tetlie et al. (2008, table 6) excepting one. However, with the exception of the Kokomo, Indiana, Wabash Formation assemblage, which is considered to be a death assemblage (Clarke and Ruedemann 1912; Tetlie et al. 2008), most values for the remaining localities are low (e.g., 1–2), and were interpreted as indicative of a molt assemblage by Tetlie et al. (2008).

The values calculated for the CSAI and CAAI yielded respective values of 4.81 ( $n = 62$ ) and 2.10 ( $n = 28$ ). These values are comparable to those calculated by Tetlie et al. (2008) for *E. remipes* from the Ellicott Creek Breccia Member (Fiddler's Green Formation) of the R.E. Law Quarry, Ontario (CSAI = 5.40; CAAI = 1.60; Tetlie et al. 2008, table 6), considered to be a molt assemblage. The Ellicott Creek Breccia Member is thought to represent a shallow, low-energy sub- to intertidal setting (Brett 1989; Vrazo et al. 2013), similar to the lower and upper units of the Tonoloway Formation. The ECI value calculated for the Ellicott Creek Breccia Member assemblage (3.56), on the other hand, is much greater than that calculated for the Winfield Quarry assemblage.

## DISCUSSION

### Paleoenvironmental Reconstruction

The fine-grained, clay-rich micrite and calcareous shale units, low-amplitude symmetrical ripple marks, microbial mounds, thin shale laminae, desiccation cracks, small-scale evaporitic structures (e.g., vugs),

and overall paucity of bioturbation and current-generated structures suggest that the exposure of the Tonoloway Formation at Winfield Quarry principally represents a shallow, restricted, and low-energy intertidal to shallow subtidal environment such as a mudflat or sabkha with variable salinity. This is consistent with previous interpretations of the upper Tonoloway Formation (Tourek 1970; Smosna et al. 1977; Smosna and Warshauer 1981; Cotter and Inners 1986; Inners 1997; Bell and Smosna 1999; Hess 2008; Elick et al. 2009).

Within this broader paleoenvironmental characterization, three distinct depositional facies associations can be identified (Fig. 3B). The desiccation cracks and vugs near the base of the outcrop (Fig. 3B; Supplementary Data Fig. 1C) are consistent with deposition within a high intertidal to supratidal setting. The suprajacent thrombolite bed records an initial deepening (transgression) (Fig. 3D, E). The thinly laminated eurypterid- and leperditicopid-bearing calcareous shale units then mark the beginning of the next facies association (Fig. 4A–C), interpreted as being deposited in a lower intertidal to shallow subtidal setting. This facies association is followed lastly by thicker, ripple-marked, and increasingly fossiliferous micrite, packstone, and rudstone units (Fig. 4D–F) which we interpret as being deposited in a subtidal setting. Combined, these three facies associations record a transgressive, upward-deepening sequence that begins with the initial flooding surface at the transition of the thrombolite bed, continues within the eurypterid-bearing shale beds, and culminates with subtidal facies associations that precede the less restricted and predominantly subtidal Keyser Formation.

The faunal diversity of Winfield Quarry supports these environmental interpretations and is comparable to that seen at other localities. Descriptions of the inferred tidal mudflat facies associations of the Tonoloway Formation in West Virginia (Smosna et al. 1977; Smosna and Warshauer 1981) and Pennsylvania (Bell and Smosna 1999) all note the same assemblage of leperditicopids, gastropods, and bryozoan fragments that is seen in the eurypterid-bearing beds at Winfield Quarry. This fauna is also broadly similar to that of the Syracuse Formation of New York, interpreted as a shallow, highly restricted tidal setting occasionally inundated with evaporitic brines (Leutze 1961). A greater diversity of eurypterids, other arthropods, and molluscs is known from the latter unit compared to the Tonoloway Formation, but, as at Winfield Quarry, eurypterids (including *Eurypterus*) and abundant leperditicopids are the predominant taxa. Farther afield, in what are interpreted as intertidal flat deposits of the upper Silurian (Ludlow) Leopold Formation of the Canadian Arctic, Jones and Dixon (1974) and Jones and Kjellesvig-Waering (1985) describe a faunal assemblage strikingly similar to that of Winfield Quarry. This assemblage includes eurypterids (*Eurypterus*, syn. *Baltoeurypterus*; Tetlie 2006), gastropods (*Hormotoma*), ostracods, and leperditicopids (*Leperditia*), and less common corals (including *Favosites*), bryozoans, and orthoconic nautiloids, as well as brachiopods.

**Paleosalinity.**—The frequent occurrence of Ordovician and Silurian eurypterids in restricted marginal settings that may have fluctuated between brackish, normal marine, and hypersaline conditions, and the resultant difficulty in assigning a preferred habitat or salinity to individual groups has long been known to paleontologists. Within eurypterid-bearing units in the upper Silurian northern Appalachian basin, for example, Alling and Briggs (1961) and Leutze (1961) both noted the difficulty in inferring paleo salinity at the bed level due to the frequent lack of fossil or sedimentary evidence, in spite of the traditional interpretation of many eurypterid-bearing intervals in this region as predominantly hypersaline (Braddy 2001).

As to the north, the prevailing sedimentological features (e.g., desiccation cracks, evaporitic vugs, syneresis cracks) throughout much of the Tonoloway Formation in Pennsylvania, including those found at Winfield Quarry and Atkinson Mills, indicate that salinity in this environment was variable, and undoubtedly hypersaline at times.

Furthermore, the Tonoloway Formation passes laterally into the Syracuse and Camillus Formations, both of which contain thick evaporite deposits of halite and gypsum. And yet, within the eurypterid-bearing beds at Winfield Quarry and Atkinson Mills, limited faunal diversity and a lack of bioturbation only imply stressed conditions, but do not directly suggest either elevated or brackish salinity levels.

The fauna offer some secondary evidence for paleosalinity and environmental conditions. Vannier et al. (2001) suggested that a monospecific distribution of leperditicopids on bedding surfaces (such as in the Tonoloway Formation) was an indication of periods of growth in low-energy environments (e.g., a tidal flat) where sediment influx was limited. Likewise, Warshauer and Smosna (1977) and Smosna and Warshauer (1981) interpreted the *Leperditia*-dominated communities within the lower and upper units of the Tonoloway Formation of West Virginia as an indication of low-energy, stressed, and possibly hypersaline environments that were frequently subjected to subaerial exposure. The abundance of leperditicopids across multiple horizons at Winfield Quarry seems to indicate that these beds were deposited under similarly stressed conditions with variable or hypersalinity.

*Eurypterus* has been variously reported from units interpreted as brackish–freshwater (e.g., Kjellesvig-Waering 1950) and highly hypersaline (e.g., the Ellicott Creek Breccia and others, see Ciuca 2011). However, we believe that sedimentary indicators of hypersalinity (e.g., salt hoppers) in the latter example may have been formed within the sediment post-burial (i.e., they are early diagenetic features), rather than being coeval with the eurypterids and cannot be taken as direct evidence that eurypterids lived under hypersaline conditions. Other limitations on possible eurypterid salinity tolerance can be gained from comparisons to modern marine chelicerates, e.g., horseshoe crabs. The latter are euryhaline and can tolerate elevated salinity levels (Ehlinger and Tankersley 2004), but have a preferred salinity range well beneath that required for evaporite formation (i.e., brines > 80 ppt). When taking into consideration the stratigraphic position of the eurypterid beds at Winfield Quarry and Atkinson Mills—above supratidal strata containing desiccation features and below a subtidal succession containing more diverse marine taxa—it seems plausible that salinity was euhaline, or somewhat elevated at the time of their burial, but probably not hypersaline.

Variable salinity may not have been the only stressor in these environments. Dysoxic or anoxic, frequently associated with the low-energy, hypersaline environments of other Silurian and Ordovician eurypterid Lagerstätten (Kluessendorf 1994; Young et al. 2007), may have played a role in reducing faunal diversity while also increasing the likelihood of soft tissue preservation (see below). Although there is no direct evidence for dysoxia/anoxia at Winfield Quarry or Atkinson Mills, the extremely gentle slope of the Tonoloway Formation's carbonate ramp (which probably extended laterally for tens of kilometers; Bell and Smosna 1999), combined with irregular tides, minimal oceanic influx, and an arid climate would have occasionally led to stagnant bodies of water where only highly tolerant leperditicopids may have been able to survive. These stressed conditions in the shallowest part of the mudflat may have been punctuated by periods of reduced salinity/increased oxygenation due to storms/rain, freshwater runoff, or minor transgressions (cf. Leutze 1961), and it was probably during these intermittent periods of freshening that eurypterids (and associated eurytopic fauna) preferentially occupied these settings (see below for further discussion).

**Taphonomy.**—The abundant, often well-preserved eurypterids at Winfield Quarry (and by extension, Atkinson Mills) suggest either a molt or death assemblage. Evidence for eurypterid mortalities is traditionally limited and equivocal (e.g., Sarle 1903; Störmer 1955; Heubusch 1962; Andrews et al. 1974; Copeland and Bolton 1985; Braddy et al. 1995; Tetlie et al. 2008) and often difficult to prove. Unequivocal

death assemblages, such as in the Silurian-age Kokomo Limestone (Indiana) (Clarke and Ruedemann 1912; Tetlie et al. 2008) and Pentland Hills (Scotland) (Anderson et al. 2007; Lamsdell 2011) Lagerstätten are rare in the fossil record. Conversely, eurypterid molt assemblages occur more commonly (although, notably, at nowhere near the frequency of other contemporaneous arthropods such as trilobites), as do the morphological features used to identify molted remains (Tetlie et al. 2008, table 1). Eurypterids, like all arthropods, molted multiple times during their lifespan (Andrews et al. 1974) and shed exoskeletons would have outnumbered living (or dead) individuals at any given time. That being said, molts are far more delicate than carcasses, and also subject to scavenging (albeit to a lesser extent than carcasses), ultimately limiting their potential for preservation. Nevertheless, they appear to form the bulk of the eurypterid fossil record.

The molting features cited earlier, low ECI value, and highly disarticulated nature of the assemblage suggest that most molts were subjected to tidal activity or storms prior to burial. The lack of tidal structures (e.g., tidal bedding, herringbone cross-stratification, etc.) other than lamination and lack of diagnostic storm indicators (e.g., graded beds, coarse-grained lags, or wave-generated structures such as hummocky cross-stratification) within the eurypterid-bearing horizons at either Winfield Quarry or Atkinson Mills prevents us from ruling out either process, and both may have played a role in specimen disarticulation. That being said, the well-preserved laminae, overall lack of coarse lags/grading/structures, and excellent preservation of nearly complete eurypterids seem to indicate that tidal processes may have been the more overarching influence, even if the tides themselves were amplified mainly by wind, or distant storms. Storms may explain the rare stenotopic taxa such as nautiloids and bryozoans that occur in the eurypterid-bearing units but were most likely washed in from deeper settings.

Compared to the ECI, the CSAI and CAAI values are relatively high, suggesting that for some specimens environmentally driven disarticulation was minimal. Together, the low ECI value, and high CSAI and CAAI values suggest that some degree of time averaging is responsible for the range of specimen completeness at Winfield Quarry. *In situ* time averaging is also supported by the wide range of leperditicopid instar sizes found on the same horizons as the eurypterids: Vannier et al. (2001) considered mixing of small and large leperditicopid instars an indication of a lack of significant transport following ecdysis (or death) over an extended period of time.

But how much time do the eurypterid-bearing shale units represent? Although the eurypterid specimens contain no original or vestigial cuticle as has been documented at other localities representing similar depositional environments (Gupta et al. 2007; Cody et al. 2011), the exuvial remains at Winfield Quarry are, for the most part, preserved in great detail, and, overall, burial must have occurred shortly after ecdysis in order to inhibit breakdown of exoskeletons by chitinoclastic bacteria. Studies on modern chitinoclastic bacteria indicate that complete degradation of chitin can take place within a week to several months depending on environmental factors such as oxygen levels, salinity, temperature and pH (Zobell and Rittenberg 1938; Seki and Taga 1963a, 1963b; Seki 1966; Gooday et al. 1991; Poulicek and Jeuniaux 1991). Marine-based chitinoclastic bacteria are inhibited by the same anoxic and very low or very high salinity conditions (i.e., freshwater–brackish, or briny) that limit soft-tissue destroying scavengers and bioturbators. Although there is no direct evidence for dysoxia/anoxia at Winfield Quarry, the lack of bioturbation, limited faunal diversity, and abundance of chitinous exoskeletons do suggest variable or non-normal marine salinity, and/or dysoxic or anoxic conditions (see above). Under these fluctuating conditions, it seems plausible that the timeframe between the shedding of the first (and presumably most degraded) molts and later, best-preserved specimens was short, perhaps a few weeks to a month.



**Trace Fossils.**—The traces found on one of the eurypterid fossil horizons at Winfield Quarry may have been formed through a variety of animal–substrate interactions. Paired tracks may have been created by swimming animals brushing against the substrate (e.g., Fig. 8A; Fig. 8B, top-right) or pushing off from the substrate (e.g., Fig. 8B, lower-left) with their swimming legs (appendage VI). The chevron-shaped markings may have been produced by stationary animals balancing on the substrate while being laterally shifted by currents (e.g., Fig. 8C–D). The patchwork of drag columns may have been caused by shed exuviae as they drifted in the water column following ecdysis (e.g., Fig. 8A). Taken as a whole, we interpret these traces as chelicerate tracks, most likely from eurypterids, created in the immediate vicinity of the molting site.

The sharp preservation of tracks at this locality may be the result of microbial activity. Seilacher et al. (1985) and Seilacher (2008) posited that microbial mats on paleosubstrates could lead to the preferential preservation of arthropod trackways (or, more likely, undertracks) that might not otherwise be preserved in the sediment. Fernández and Pazos (2013) suggested a similar method of preservation for xiphosuran trackways in a subaerial beach deposit from the Cretaceous. Aside from the thrombolites and probable rippled microbial structures under- and overlying the eurypterid-producing beds (Supplementary Data Fig. 1C), secondary evidence for the presence of microbial mats in the Tonoloway Formation is the abundance of gastropods and leperditicopids on some horizons. These organisms may have found a plentiful food source in the bacterial mats (Smosna et al. 1977).

If the tracemakers were eurypterids, this would be the first documented example of eurypterid trace and body fossils co-occurring on the same horizon. There are numerous examples of trackways ascribed to eurypterid producers (e.g., Briggs and Rolfe 1983; Braddy and Milner 1998; Draganits et al. 2001; Whyte 2005; Poschmann and Braddy 2010; Morrissey et al. 2012), but body and trace fossil associations are not previously reported. Possible arthropod swimming traces, potentially eurypterid in origin, are known from the upper Silurian Williamsville Formation A unit (*sensu* Ciuca 1990) in Ontario, but these occur as hypichnial traces on the undersides of slabs bearing eurypterid fossils (Ciuca 2002). Eurypterid body fossils and putative eurypterid trackways (cf. *Palmichnium*; Braddy 2001, fig. 3) are also purportedly found in close association within the lower Silurian Whirlpool Formation of Ontario, but these are only known from float and the exact source horizons are unclear (D.M. Rudkin, personal communication 2013).

The co-occurrence of body and trace fossils is significant when interpreting the *Eurypterus* sp. habitat. Previous interpretations were primarily based on body fossils, a majority of which were probably molt remains (Tetlie et al. 2008). Molts, being the lightweight counterpart to the shedding organism, are easily transported and may not remain at the site of ecdysis before burial. Assuming that the tracks at Winfield Quarry are those of eurypterids, the close association of body and trace fossils appears to be primary evidence that the eurypterids preserved there were inhabitants of that environment, even if only briefly, rather than transported remains. Further, these tracks may also help constrain the potential salinity range within the eurypterid-bearing beds at Winfield Quarry. Subaqueous traces ascribed to Silurian and Devonian eurypterid producers elsewhere are typically found in environments that are interpreted as eu- or hyposaline environments (e.g., Davies et al. 2006; Marriott et al. 2009; Poschmann and Braddy 2010), rather than hypersaline (cf. Ciuca 2002).

**Paleoecology.**—As indicated by the taphonomic indices values discussed above, the eurypterids at Winfield Quarry appear to represent molt assemblages on two different horizons, with individual specimens displaying varying degrees of disarticulation. The sheer abundance of eurypterids within these two horizons contrasts sharply with the complete lack of any eurypterid material from adjacent (and well-scouted) strata.

This sudden and stratigraphically limited appearance of molts suggests an ephemeral nature to their inhabitation of this environment and the possibility that each horizon consists of specimens from separate molting events. Such an interpretation is consistent with the long-held view that Silurian eurypterids periodically sought out and congregated in shallow, restricted environments such as lagoons or tidal flats, most likely to molt (e.g., Sarle 1903; Ruedemann 1934; Caster and Kjellesvig-Waering 1964; Størmer 1976) and/or to mate/spawn *en masse* (cf. the “mass-molt-mate” hypothesis, Braddy 2001; Vrazo and Braddy 2011). It seems logical that, like its cohorts in the northern Appalachian basin, *Eurypterus* sp. would have used the restricted tidal flat setting of the Tonoloway Formation as a protective environment in which to molt. Similar mass-molting behavior has also been inferred from other Paleozoic arthropod taxa including *Canadaspis perfecta* and a megacheiran (*Alacomeneus* sp.) from the Cambrian (Haug et al. 2013), and trilobites (Speyer and Brett 1985; Karim and Westrop 2002). Mass-mating or spawning behavior among eurypterids, however, is more difficult to prove in the absence of physical evidence such as nests or equivalent traces (but see Le Herisse et al. 2012, for microfossil evidence of putative spermatophores associated with eurypterids) or behavioral evidence for mating or spawning (i.e., external transfer of a spermatophore from male to female; cf. Braddy and Dunlop 1997; Kamenz et al. 2011). Further, there is no precedent in the marine chelicerate phylogeny for coupled molting and mating/spawning (Haug et al. 2013) including within the Xiphosura, which are traditionally used as a modern analog for eurypterids. Nonetheless, the presence of juvenile molts at Winfield Quarry offers two possible scenarios (or some combination thereof): (1) both juveniles and adults migrated into these settings to molt *en masse*; (2) this shallow-water environment may have served as a nursery proximal to a breeding site (cf. Braddy 2001; Haug et al. 2013).

#### *Paleoenvironmental and Sea-Level Controls on Fossilization*

The positioning of the eurypterid-bearing beds at Winfield Quarry and Atkinson Mills just above a thrombolitic unit (indicative of early transgressive conditions) and the intertidal zone of a mudflat suggests that the fossil horizons occur slightly above the flooding surface of a regional-scale transgression that precedes the Keyser Formation. (This transgression may be correlative to the late Ludlow–early Prídolí transgression documented by Johnson et al. [1998], but higher-precision age data are needed to link the stratigraphy to these well-documented sea-level fluctuations.) We suggest that the occurrence of eurypterids within this succession is specifically due to changes in the local environment resulting from this transgression, rather than merely by chance or by storm deposition. Although we cannot entirely rule out that the beds on which the eurypterids occur simply represent one or two storm-driven deposits containing molts washed in from a deeper, subtidal setting (as discussed above), the accompanying trace fossils appear to discount this possibility. Additionally, we believe that the regional paucity of eurypterids elsewhere in the Tonoloway Formation is an indication of their preference for environmental conditions created as a result of sea-level rise. The regular cycling between sub- and supratidal successions within the Tonoloway Formation, and the frequently restricted, occasionally hypersaline conditions created therein, would be highly conducive to burial and preservation of soft tissues (Kluessendorf and Mikulic 1991; Kluessendorf 1994), but would also be hostile to all but the most tolerant organisms including, presumably, eurypterids. The appearance of eurypterids at Winfield Quarry and Atkinson Mills in only the initial portion of a deepening interval suggests that *Eurypterus* sp. was not a regular inhabitant of most nearshore settings within the Tonoloway Formation, and instead may have been tracking some ideal salinity or environmental condition created following flooding of the tidal flat (cf. Clarke and Ruedemann 1912; Leutze 1961).

In this scenario, the burial of molts in the Turbotville Member of the Tonoloway Formation at Winfield Quarry and Atkinson Mills would be the result of both environmental influences, i.e., rising sea level within a tidal mudflat setting, and behavioral traits that led eurypterids to gather in these localities *en masse*. The end result is a *Konservat-Lagerstätte* preserved within a narrow taphonomic window, but one that is not reliant on unique preservational parameters inasmuch as it is created by a normal transgressive event within a geographically broad marginal setting frequented by eurypterids. A similar pattern of sequence stratigraphic control on eurypterid occurrences has been noted in the northern Appalachian basin, e.g., in the Bertie Group of New York (e.g., Cieurca 1973, 1990), and elsewhere in Laurentia, e.g., Somerset Island, Canada (Dixon and Jones 1978; Jones and Kjellesvig-Waering 1985), and Baltica, e.g., Saaremaa Island, Estonia (Viira and Einasto 2003; Meidla et al. 2014) and this pattern warrants further study.

In summary, we conclude that the presence of eurypterids on correlative horizons at two geographically distant localities—Winfield Quarry and Atkinson Mills—is an early indication of the regional scale at which *Eurypterus* may have occurred within the central Appalachian basin, and offers further support for Kluessendorf's (1994) argument for the prospecting of additional Lagerstätten within this region. The apparent absence of eurypterids at other exposures geographically closer to Winfield Quarry is probably due to a lack of well-exposed dip slopes at these localities, rather than a preservational reality. Additional fieldwork in this region should yield more occurrences, and with them, further evidence for eurypterid inhabitation of the nearshore environment of the central Appalachian basin during the late Silurian.

#### CONCLUSIONS

1. A *Eurypterus* Lagerstätte from the upper Silurian Tonoloway Formation of Pennsylvania has provided the first evidence of mass assemblages of eurypterids in the central Appalachian basin.
2. *Eurypterus* sp. occurs within the lower intertidal to shallow subtidal zone of a mudflat or sabkha deposited along a gently dipping carbonate ramp. Associated fauna are rare and diversity is low, reflective of a restricted marginal-marine environment with variable salinity.
3. Most eurypterid specimens are disarticulated to some extent, but some are almost fully articulated. Taphonomic indices suggest a parautochthonous molt assemblage with limited transport, similar to molt assemblages in the northern Appalachian basin.
4. Trace fossils offer probable direct evidence that eurypterids may have occasionally inhabited this environment. Deposition here is probably not the result of transport from a life habitat elsewhere.
5. The preservation of a monospecific assemblage of molts from both juvenile and adult instars from one species suggests that *Eurypterus* sp. may have congregated within a quiet marginal setting for the purposes of molting, and, perhaps, mating *en masse* (cf. Braddy 2001). Juvenile instars may have also used this setting as a protective environment during early development.
6. The occurrence of eurypterids at two distant localities on correlative horizons within the transgressive stage of a stratigraphic sequence suggests that their occurrence is due to environmental preference, rather than a taphonomic artifact or bias.
7. The discovery suggests that the paucity of eurypterid specimens from the late Silurian of the central Appalachian basin may be the result of undercollecting rather than a taphonomic or ecological reality.

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#### SUPPLEMENTAL MATERIAL

Data is available from the PALAIOS Data Archive: <http://www.sepm.org/pages.aspx?pageid=332>.

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