Palaeogeography, Palaeoclimatology, Palaeoecology 444 (2016) 48–59

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Buried or brined? Eurypterids and evaporites in the Silurian Appalachian basin

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ARTICLE INFO

Article history:
Received 10 September 2015
Received in revised form 10 December 2015
Accepted 13 December 2015
Available online 21 December 2015

Keywords:
Salina/Bertie groups
Eurypterus
Salt hopper
Diagenesis
Arthropod paleoecology hypersalinity

ABSTRACT

Eurypterid-bearing deposits from the late Silurian Appalachian basin are often interpreted as having been deposited under hypersaline conditions. These interpretations are based on the close association of abundant eurypterid remains with evaporite deposits and structures such as salt hoppers in the Salina and Bertie groups. To determine whether this association reflects life habitat, or is the result of taphonomic or diagenetic processes, the co-occurrence of eurypterids and salt hoppers in the upper Silurian Appalachian basin was examined at several stratigraphic scales. A survey of eurypterid remains from the prolific Ellicott Creek Breccia Member of the Fiddler's Green Formation (Bertie Group) found that 2% of the 479 specimens surveyed are crosscut by salt hoppers or incipient halite structures. In a regional survey, displacive salt hoppers occurred in the same bed as eurypterid remains in 37% (19:51) of all eurypterid-bearing units. In these units, salt hoppers were typically the only structures found intimately associated with eurypterids, sometimes crosscutting them. The disruptive nature of the hoppers in the Ellicott Creek Breccia, for example, suggests that they formed within the sediment rather than at the air-water interface, and that organic remains might have acted as nucleation points for developing halite crystals. To explain these associations, we present a depositional model in which displacive salt hoppers formed within NaCl-saturated groundwater as a result of surface evaporation in the vadose zone during regressive phases, and only after eurypterid remains were buried. In this scenario, the intimate association of eurypterids and salt hoppers in these deposits reflects early-stage diagenetic overprinting rather than conditions during life. Our model largely refutes the hypothesis that eurypterids were halotolerant organisms based on their co-occurrence with salt hoppers. We conclude that eurypterids preserved in upper Silurian carbonate ramp deposits were primarily denizens of more normal marine or hyposaline subtidal settings.

1. Introduction

The habitats of the Eurypterida (Arthropoda: Chelicerata) have long been disputed. Although there now appears to be a consensus that eurypterids underwent a marine-to-freshwater transition during the Late Ordovician–Devonian (Lamsdell and Braddy, 2010; see O'Connell, 1916; Plotnick, 1999; Braddy, 2001, for reviews), the preferred habitat and salinity tolerance of many individual groups during this period remain unresolved. Recent work has refined our view of the taxonomic basis for this transition into terrestrially dominated settings (Lamsdell and Braddy, 2010), but a lack of constraint on the habitat range of many eurypterid lineages remains. Without these basic paleoecological details, it is difficult to ascertain not only the drivers behind this environmental transition, but also the drivers of eurypterid extinctions that began in the end-Silurian and culminated in the end-Devonian mass extinction (Lamsdell and Braddy, 2010).

Among these transitional taxa are eurypterids from the upper Silurian–Lower Devonian Salina, Bertie, and lowest Helderberg groups of the Appalachian basin of Laurentia. Here, abundant and well-preserved eurypterids and other fauna are frequently found in calcareous shales and argillaceous, chemically precipitated dolomites ("waterlimes"), deposited in what is generally considered to represent the subtidal–supratidal zone of a shallow lagoonal or sabkha-like environment on the margin of a gently dipping epeiric sea (Ciurca, 1973; Smosna et al., 1977; Belak, 1980; Hamell, 1982; Tollerton and Muskatt, 1984; Ciurca, 1990; Bell and Smosna, 1999). Despite general agreement on the depositional environment, determination of the specific paleosalinity (i.e., brackish [hyposaline], normal marine [euhaline], or hypersaline–briny) and eurypterid habitat in these settings is complicated by the co-occurrence of eurypterids with putative terrigenous flora, and normal marine and euryhaline fauna (Tollerton, 1997, and references therein; Plotnick, 1999, and references therein; Braddy, 2001;

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http://dx.doi.org/10.1016/j.palaeo.2015.12.011
0031-0182/

Burrow and Rudkin, 2014; McKenzie, 2014; Nolan, 2014; Vrazo et al., 2014b; SJC, personal observations), in units that frequently either lack defining sedimentology at the bed level (cf. Alling and Briggs, 1961; Leutze, 1961) or contain indicators of extreme hypersalinity, i.e., evaporitic salt hoppers (Ciurca and Hamell, 1994).

Because halite structures are formed under evaporative, hypersaline conditions (Dellwig, 1955; Arthurton, 1973; Southgate, 1982), their intimate association with eurypterids in nearshore deposits has led to the assertion by some authors that eurypterids (and other early chelicerates, e.g., scorpions; Kjellesvig-Waering, 1966) probably inhabited these conditions, and/or were euryhaline (e.g., Clarke and Ruedemann, 1912; Alling and Briggs, 1961; Størmer, 1976; Kluessendorf, 1994; see Braddy, 2001). However, implicit within this view is the requirement that eurypterids tolerated far higher salinities than any modern marine chelicerate.

In this study, we aim to determine the likelihood for eurypterid inhabitance, or burial, in hypersaline environments by examining the depositional relationship of eurypterids and salt hoppers at several stratigraphic scales, from locality to regional-level. Surveys of eurypterid–salt hopper associations provide empirical evidence for the respective timing of eurypterid burial and associated evaporite formation, and whether or not these structures should be considered indicative of habitat salinity. Based on these results, we present a new depositional model to explain the co-occurrence of eurypterids and evaporites in the Appalachian basin, and discuss its implications for eurypterid life habitats and preservation in the mid-Paleozoic.

2. Geologic setting

2.1. Appalachian basin stratigraphy

Laurentian epicontinental seas during the mid-Paleozoic were frequently evaporitic (Rickard, 1969). In the Appalachian basin, restricted oceanic input, a low latitude position, and a warm, arid climate led to the formation of evaporite deposits often hundreds of meters thick in the basin depo-center (Alling and Briggs, 1961; Dennison and Head, 1975; Smosna et al., 1977; Van der Voo, 1988). These evaporite deposits are represented by subsurface formations in the Salina Group lettered A–F (Rickard, 1969). Nearshore carbonate ramp environments in the northern Appalachian basin (New York and Ontario) are represented by exposures in the Syracuse and Camillus Formations (Salina Group) and the entire Bertie Group (Fig. 1). To the south, in Pennsylvania, Maryland, and West Virginia, this ramp setting is represented by the more argillaceous Wills Creek and Tonoloway Formations (Tourek, 1970 unpublished; Bell and Smosna, 1999). The Bertie Group contains none of the thick evaporite deposits seen in the Salina Group and, evidently, the basin was less prone to significant evaporite formation than it had been during Salina deposition. However, the basin still became hypersaline or briny during Bertie Group deposition, as indicated by the presence of thin evaporite layers such as the gypsum beds in the Forge Hollow Formation, and various evaporitic structures (Tollerton and Muskatt, 1984; Ciurca and Hamell, 1994).

2.2. Paleosalinity

Paleosalinity in the carbonate ramp settings of the upper Silurian Appalachian basin has been interpreted as ranging from brackish to hypersaline or briny. Brackish conditions are usually inferred from circumstantial evidence such the presence of terrestrial flora, a paucity of euhaline marine fauna and bioturbation, and the presence of apparently euryhaline, hyposaline-tolerant taxa such as gastropods, brachiopods, ostracods, and leperditicopid arthropods (e.g., Kjellesvig-Waering, 1950; Leutze, 1961; Plotnick, 1999; Vannier et al., 2001; Edwards et al., 2004; Vrazo et al., 2014b). Lingulate brachiopods are often found with eurypterids and are suggestive of eu- or hyposalinity as none have been identified in unequivocally hypersaline settings. The extinct ostracod-like arthropod *Leperditia* is particularly abundant in some mid-Paleozoic eurypterid assemblages, and is thought to have been both highly halotolerant and resistant to desiccation (Vannier et al., 2001). However, leperditicopids are frequently found in isolation on bedding planes within subaerially exposed sabkha-like intertidal–supratidal zones (e.g., in the Tonoloway Formation; Smosna et al., 1977; Warshauer and Smosna, 1977; Vrazo et al., 2014b), suggesting that they were more tolerant of evaporative conditions than other contemporaneous arthropods, including eurypterids. Eurypterids themselves have previously been used as indicators of hyposalinity in some settings, but it has since been argued that, in the absence of other sedimentological evidence, such interpretations may be erroneous because of their euryhaline tendencies (Selden, 1984; Braddy, 2001).

Unlike brackish conditions, hypersalinity in Appalachian basin nearshore deposits is unequivocally indicated by evaporitic structures such as gypsum beds, casts, and vugs, salt hoppers or halite molds/casts, and desiccation features, e.g., desiccation cracks, that occur throughout the Salina Group and suprajacent Bertie Group (Hamell, 1982; Hamell and Ciurca, 1982; Tollerton and Muskatt, 1984; Ciurca and Hamell, 1994). Salt hoppers and early-stage halite molds/casts (i.e., flat-faced cubic halite impressions lacking the characteristic hopper shape; see below) are among the most common sedimentary features in these intervals and both types of structure frequently occur on the same bedding planes as eurypterids (Tollerton and Muskatt, 1984; Ciurca and Hamell, 1994; Ciurca, 2013; see below), sometimes even crosscutting them or other organic structures. This close eurypterid–evaporite association has led some authors to suggest that pervasive hypersalinity may have been conducive to the excellent preservation of eurypterids and other fauna in the Bertie Group (Leutze, 1961; Kluessendorf, 1994; Edwards et al., 2004; Vrazo and Braddy, 2011; Ciurca, 2013). Although unwilling to make any definite claims regarding eurypterid salinity tolerance, Leutze (1961) went as far as to suggest that high salinity in the Salina Group may have occasionally created a “pickling brine”, preserving tissue that was otherwise unlikely to survive bacterial degradation. Because of the particularly close association of salt hoppers with eurypterids, we will focus on their development below.

2.3. Salt hopper development

Salt hoppers are hopper-shaped crystalline structures made from evaporitic minerals (halite) that occur in both ancient and modern settings. The term “hopper” refers to the stepped, pyramidal shape that is formed as the mineral precipitates outward from the edge, rather than center, of a crystal core. Salt hoppers are only one of several types of halite structure that have been found in Laurentian evaporite deposits and should not be confused with chevron halite, for example (Dellwig, 1955; Arthurton, 1973). Hopper-shaped halite crystals have been shown to form experimentally both at the air-water interface in saturated sodium chloride (NaCl) brines (Dellwig, 1955; Arthurton, 1973; Southgate, 1982) and within the water column (Sloss, 1969) as a result of surface evaporation. In the field, these are traditionally interpreted as having formed in evaporitic brine pools (e.g., Southgate, 1982). If halite crystals, either as an isolated hopper or as part of a floating crystalline raft, become too large to be kept buoyant by surface tension, they will drop down to the substrate and continue to grow as bottom growth crystals if the water column is completely saturated (Dellwig, 1955). Salt hoppers may also grow within the sediment if sodium chloride-saturated brines laterally penetrate the phreatic or vadose zone of subaerially exposed deposits (Gornitz and Schreiber, 1981). Evidence for displacive intrasedimentary salt hopper growth in the subsurface has been noted in modern or sub-Recent basins (Gornitz and Schreiber, 1981), sabkhas (Shearman, 1978), and salt pans and lakes (Handford, 1982; Lowenstein and Hardie, 1985), and in ancient marine sediments (Leitner et al., 2013).

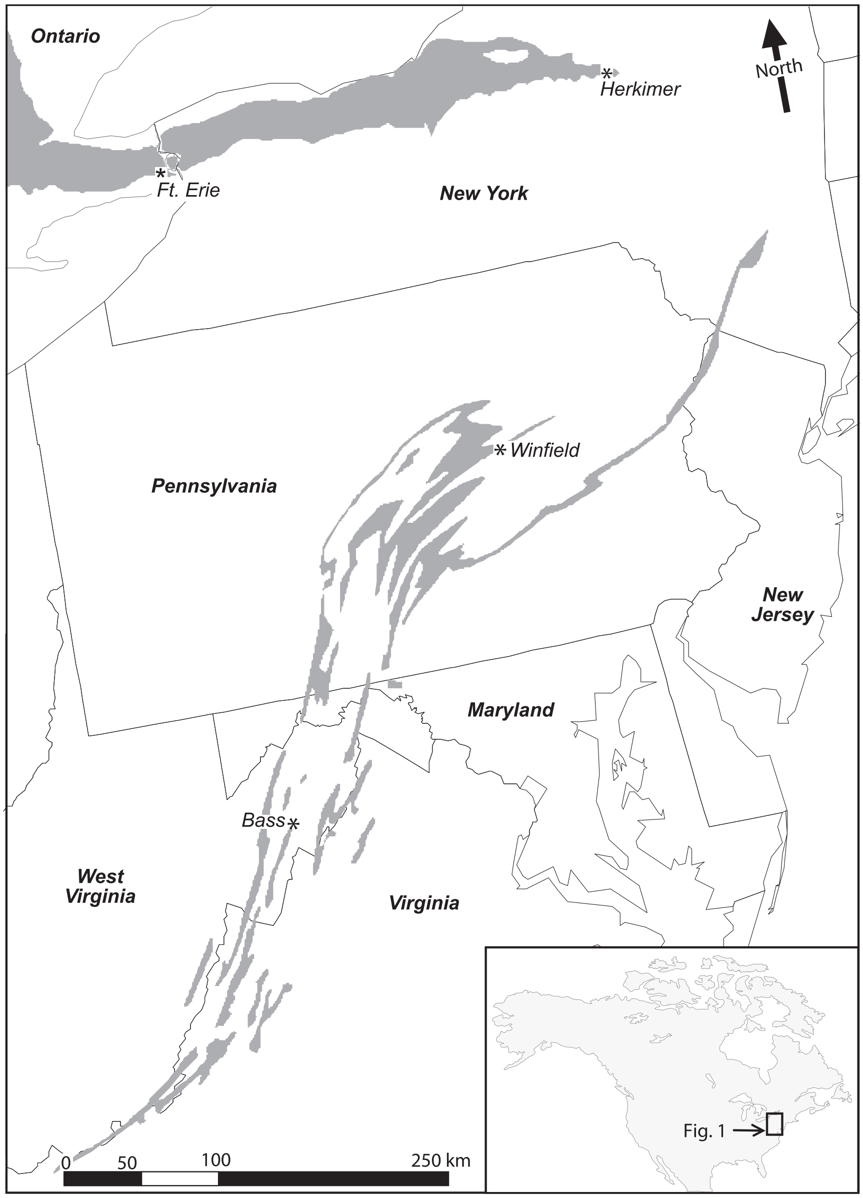

Fig. 1. Regional map of North American Appalachian basin and study area. Silurian bedrock exposures are represented by the shaded area; key localities are starred. Herkimer and Ft. Erie mark the approximate bounds of the field area for the northern Appalachian basin; Bass and Winfield indicate the approximate extent of the field area in the central–southern Appalachian basin. Modified from Vrazo et al., 2014b.

2.4. Salt hoppers in the Appalachian basin

In Silurian surface exposures in the Appalachian basin, salt hoppers appear to always be replaced by a relict, pseudomorph mold, or cast, that retains the “hopper” or pyramidal shape of the original crystal structure (e.g., Fig. 2). Salt hoppers in subsurface exposures, however, can retain their original halite composition (SJC, personal observation). The color of the infill of many salt hopper pseudomorphs ranges from bright orange to purple-red, indicating incorporation of iron at the time of formation or during subsequent replacement (Dellwig, 1955; Ciurca and Hamell, 1994) (Fig. 2A–C). Other salt hopper pseudomorphs are metallic or white, having been replaced with hematite, dolomite, or quartz, respectively (e.g., Fig. 2D–E). Unaltered salt hoppers are entirely absent from any exposures examined during this study and thus we will refer to pseudomorph casts or molds simply as salt hoppers herein.

The salt hoppers found in the eurypterid-bearing units in the upper Silurian units of the Appalachian basin are notable both for their size, some growing upward of 30 cm (Ciurca and Hamell, 1994), and their isolated nature. Unlike those that are found as part of the thick and widespread evaporite beds that are found in the subsurface Salina Group (e.g., Dellwig, 1955), salt hoppers in surface exposures, for example, in the Phelps Waterlime Member (PWM) at Neid Rd. Quarry, NY, appear sporadically within a dolomitic matrix. Based on current models, these salt hoppers developed either: 1) at the brine surface, and subsequently dropped to the bottom once they became larger, as suggested by Dellwig (1955) for some larger salt hoppers in the Michigan basin, 2) as isolated bottom-growth crystals on the substrate (cf. Dellwig, 1955; Arthurton, 1973), or 3) interstitially within the sediment (cf. Gornitz and Schreiber, 1981; see below).

2.5. Salt hopper–eurypterid/organismal associations

The observation that eurypterids are closely associated with evaporites in the upper Silurian was made early in their study (e.g., Clarke, 1907). Subsequent authors have considered the possible eurypterid occupation of hypersaline or briny environments in the context of

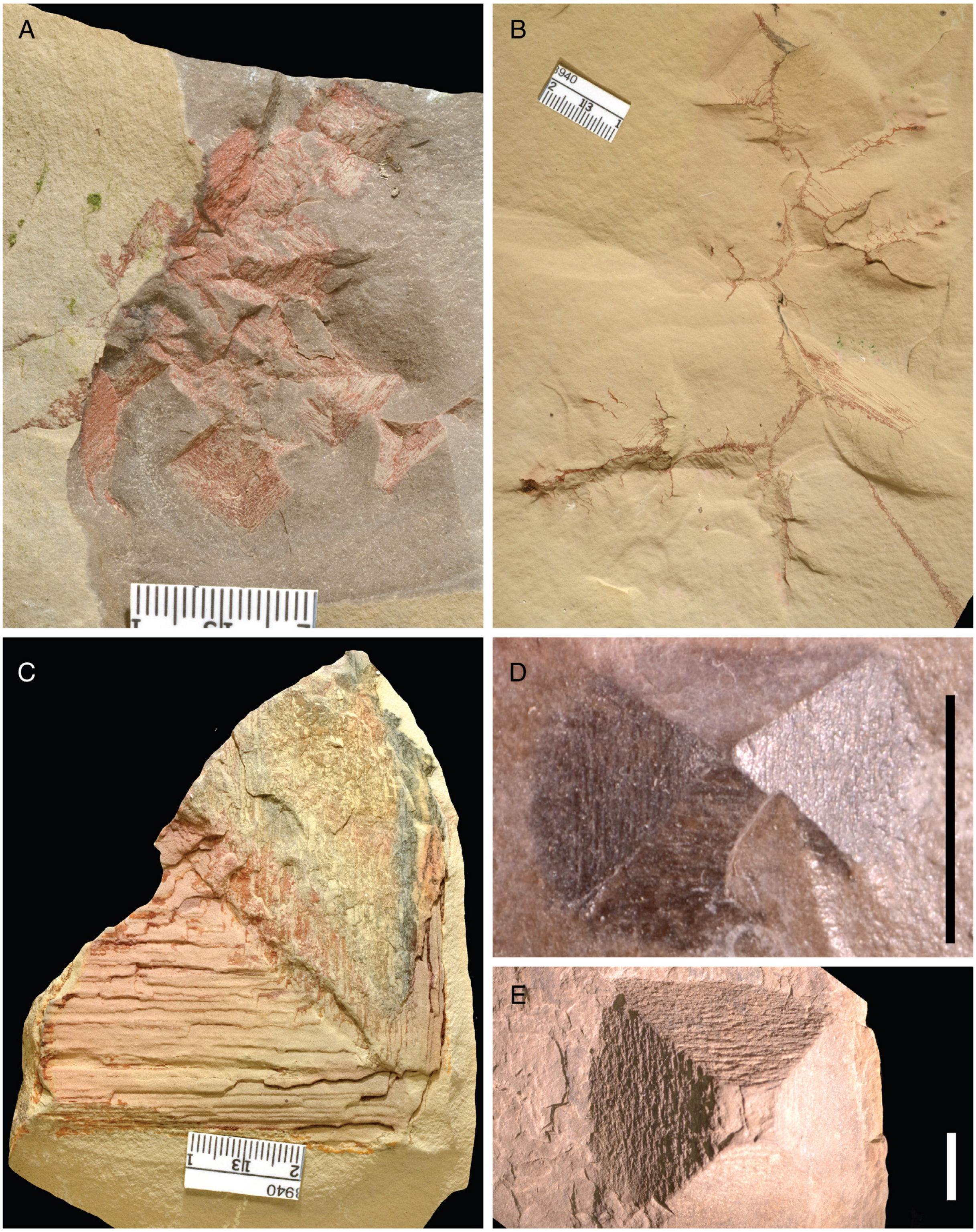

Fig. 2. Evaporitic structures from the Fiddler's Green Formation of New York and Ontario. Scale bars = 1 cm; scales in cm. A) Salt hopper pseudomorphs from the Phelps Waterlime Member, Neid Rd. Quarry, New York. B) Converse (top) side of A; red evaporitic dendrites visible. C) Isolated salt hopper pseudomorph from the Phelps Waterlime Member, Neid Rd. Quarry, New York. D) Isolated salt hopper pseudomorph from the Ellicott Creek Breccia Member, Ridgemount Quarry, Ontario (YPM #215039). E) Isolated salt hopper pseudomorph from the Ellicott Creek Breccia Member, Ridgemount Quarry, Ontario (YPM #212443) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

eurypterid paleoecological trends during the Paleozoic (e.g., Clarke and Ruedemann, 1912; O'Connell, 1916; Kjellesvig-Waering, 1961; Størmer, 1976; Plotnick, 1999; Braddy, 2001), but comparatively little attention has been given to the physical co-occurrence of evaporitic structures and eurypterids. Tollerton and Muskatt (1984) provided an in-depth review of sedimentary structures in the Bertie Group, including evaporites. They inferred that halite crystals may have formed at very shallow depths in this environment, but left open the question of water depth and did not specifically consider salt hoppers in relation to eurypterid inhabitation or preservation. The only documented example of a close eurypterid–salt hopper association in the Salina Group was by Ciurca (1990; personal observation), who found salt hoppers and eurypterids on the same horizon, including a salt hopper disrupting a fossil exoskeleton, in what they termed the Barge Canal Member of the Vernon Formation (located above Sarle's [1903] "Pittsford shale" eurypterid assemblage [cf. Hartnagel, 1903]). In the Bertie Group, Ciurca (2005, 2011, 2013) and Ciurca and Hamell (1994) documented examples of salt hoppers that cross cut various organisms. In the Moran Corner Waterlime,

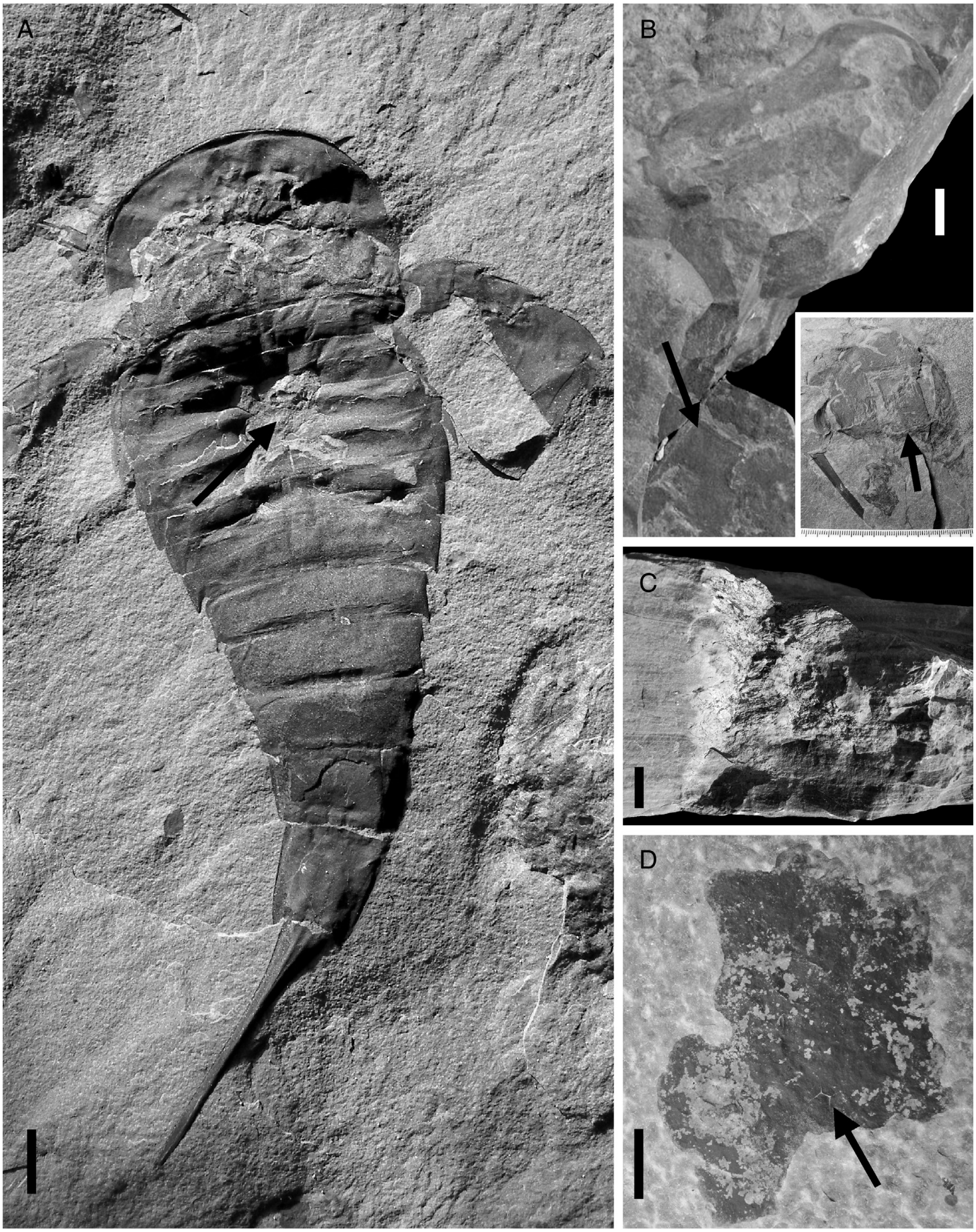

Fig. 3. Examples of evaporitic structures crosscutting biogenic structures in the Bertie Group. Scale bars = 1 cm; scales in cm. Arrows indicate salt hoppers. A) Eurypterid (*Eurypterus*) with disruptive salt hopper pseudomorph in pre-abdomen, Moran Corner Waterlime (post-Akron Formation, Bertie Group), Moran Corner, New York. B) Nautiloid cephalopod and putative salt hopper pseudomorphs, unnamed bed beneath Williamsville–Akron Formation boundary, Farmington, New York. Inset: cephalopod with disruptive salt hopper pseudomorph, and eurypterid (*Eurypterus*?) telson, A Member, Williamsville Formation, Ridgemount Quarry, Ontario. C) Thrombolite with disruptive halite evaporite, Fort Hill Waterlime, near LeRoy, New York. Modified from Ciurca, 2013. D) Black organic material (microbial?) with salt hopper pseudomorph, A Member, Williamsville Formation, Ridgemount Quarry, Ontario. Modified from Ciurca, 2013.

Ciurca collected a eurypterid that had been disrupted by a salt hopper (Fig. 3A). In the Fort Hill Waterlime, Ciurca (2011, fig. 1) highlighted a microbial mound (thrombolite?) growing on top of a salt-hopper-bearing dolomite and a rare disruptive salt hopper growing within a thrombolite (Fig. 3C). In the Ellicott Creek Breccia Member (ECB), Ciurca (2013, fig. 17) documented a large salt hopper on the same bedding plane as eurypterid remains. From the Williamsville Formation, Ciurca collected slabs containing cephalopods with putative salt hoppers growing either within, or adjacent to them (Ciurca, 2010, fig. 36; Fig. 3B), and found an example of small salt hopper displacing what may be a microbial mat (Fig. 3D).

3. Eurypterid and chelicerate physiology

Testing any hypothesis that eurypterids occupied hypersaline environments first requires assessment of the likelihood that eurypterid remains in these settings represent some sort of autochthonous assemblage, contemporaneous with the evaporite evidence, and available physiological evidence for halotolerance. A variety of taphonomic and stratigraphic evidence indicates that eurypterids were regular inhabitants of upper Silurian nearshore carbonate settings in which they are found (rather than products of periodic storm deposition, but see Andrews et al., 1974) and that they were regionally widespread (rather than isolated within “pools”, cf. Clarke and Ruedemann, 1912). The evidence includes results from a taphonomic census (Tetlie et al., 2008); the unsorted size-frequency distribution of eurypterid populations (Kaneshiro, 1962 unpublished; Andrews et al., 1974; Vrazo and Braddy, 2011; Vrazo et al., 2014b); the regular preservation of very small (juvenile) eurypterid instars, often with adults (cf. Clarke and Ruedemann, 1912; Ruedemann, 1925; MBV, personal observation); the continuous occurrence of some taxa within exposures across large geographic distances (up to hundreds of miles) (SJC, personal observations); and the cyclic recurrence of Bertie Group eurypterid assemblages within similar dolomitic facies (Ciurca, 1973).

In contrast, physiological evidence for eurypterid and chelicerate occupation of hypersaline environments is less compelling. The only documented eurypterid adaptation to hypersalinity comes from *Tylopterella (Tylopterus) boylei*. Known from only one specimen from the Guelph Formation of New York, Clarke and Ruedemann (1912, p. 218) (and, later, Kjellesvig-Waering, 1958) suggested that the thickened cuticle of this rare taxon was evidence for its inhabitation of “very saline water”. However, the lack of this character in other eurypterid taxa that occur in hypersaline settings suggests that either the interpretation of the cuticle's purpose, or the proposed depositional environment, is incorrect. Recently, Lamsdell et al. (2009) and Lamsdell and Braddy (2010) suggested more convincingly that the large body size and thick exoskeletal cuticle of giant hibbertopterids in the late Paleozoic were adaptations toward brackish or freshwater habitats, leaving open the question of physiological adaptations to hypersalinity.

In a broader paleoecological context, evidence for eurypterid inhabitance of hypersaline conditions is similarly equivocal. Kjellesvig-Waering's (1961) once generally accepted “phase” model that grouped eurypterid taxa based on their apparent environmental preference, e.g., the Eurypteridae occurred in restricted environments prone to hypersalinity, has since been shown to be oversimplified (Braddy, 2001). No single taxon or group shows a consistent preference for hypersaline settings. Those taxa that appear most frequently in hypersaline nearshore settings in the upper Silurian also appear in less extreme settings elsewhere. These include *Eurypterus*, which has been found as part of a normal, open marine death assemblage (Lamsdell, 2011); dolichopterids, which have been found in both brackish or near normal marine environments (Kjellesvig-Waering and Leutze, 1966; Vrazo et al., 2014b); and the large pterygotids, which are frequently found alongside *Eurypterus* in hypersaline deposits but are thought to have been capable of traversing open oceans (Tetlie, 2007).

Examination of halotolerant capabilities in modern analogs also does not support eurypterid inhabitation of hypersaline environments. Xiphosurids are the extant marine chelicerate clade most closely related to eurypterids and have traditionally been used for comparison in studies of eurypterid paleoecology and physiology. In their natural habitats, modern xiphosurids such as *Limulus polyphemus* are euryhaline and can tolerate brackish–mildly hypersaline conditions (Shuster, 1982). Ehlinger and Tankersley (2004) showed experimentally that larval *Limulus* populations can tolerate salinities up to 70 ppt, but begin to decline in higher salinities (i.e., 80 ppt; “penesaline” brines). *Limulus* also appears to become less halotolerant as it ages and no limulid species is known to occupy briny bodies of water at any growth stage in natural habitats. Following Waterston's (1979) observation that decapod crustaceans are increasingly halotolerant in warmer climates, Selden (1984) suggested that eurypterids may have had a wider salinity range than xiphosurids, particularly in the lower, warmer latitudes of Laurentia. Although Ehlinger and Tankersley (2004) did find an increase in halotolerance in larval *Limulus* when subjected to increased temperatures, viable salinity levels remained beneath that of brines and well beneath the salinity level required for halite evaporite production (~350 ppt; Scruton, 1953).

4. Analysis of eurypterid–evaporite associations

To assess the frequency of eurypterid–evaporite associations quantitatively, fieldwork was carried out from 2012–present at a number of key localities across the Appalachian basin: from the south, e.g., Bass, WV, to the north, e.g., Litchfield, NY, and through exposures to the west, e.g., Ridgemount Quarry, ON. Observations made in the field were combined with additional field notes made by one of us (SJC) to create a comprehensive picture of bed-level occurrences of eurypterids and evaporitic structures within a regional stratigraphic context. To supplement field observations, surveys of eurypterid–salt hopper associations were carried out at the locality-specific scale, and at the regional scale.

4.1. Locality-specific survey

Specimens from the ECB of the Fiddler's Green Formation (Bertie Group) of southwestern Ontario were surveyed for eurypterid–salt hopper associations. This unit was chosen because of the large number of eurypterids (>800) that have been collected from this interval by SJC from a single locality (Ridgemount Quarry, near Ft. Erie, ON; 42°92′N/79°00′W), the presence of salt hoppers throughout the unit, and its traditional interpretation as a hypersaline environment (e.g., Ciurca, 2013). The ECB is a roughly three-meter thick dolomitic unit deposited within the subtidal–intertidal zone of a shallow carbonate ramp. The “breccia” refers to a collapsed breccia layer that is found in the upper ECB throughout its exposure (southwestern Ontario to western New York), which is either the result of evaporite dissolution, a seismite, or both (cf. Ciurca, 2011). Eurypterids are found throughout the ECB, but occur predominantly within the lower and middle sections of the unit within large microbial/thrombolitic beds that Ciurca (2011) refers to as a topographic waterlime.

Specimens collected from the ECB and examined in this study were predominantly *Eurypterus* cf. *remipes*, with a smaller number of *E.* cf. *laculatus* (cf. Tetlie, 2006). Other taxa known from this interval include dolichopterid, pterygotid, and carcinosomatid eurypterids, as well as athyrid brachiopods (*Nucleospira*), nautiloid cephalopods (*Hexameroceras*), and unidentified ostracods or leperditicopids (MBV, personal observation). Most *Eurypterus* in the ECB are represented by isolated carapaces; complete or partially articulated examples are rare. Several specimens of *Eurypterus* cf. *remipes* used in this study were collected in the field in the summer of 2014, but the majority of specimens are housed at the Yale Peabody Museum (YPM) in the Ciurca Collection. This collection contains over 10,000 specimens of eurypterids collected by one of us (SJC) from the 1960s to the present. SJC typically collected all eurypterid specimens (including disarticulated tagma and isolated fragments), as well as associated fauna and sedimentary structures, from a given locality. Thus, the breadth of this collection and generally limited collector bias permit detailed censuses of eurypterid remains to be carried out (Tetlie et al., 2008; Vrazo et al., 2014b).

4.2. Region-wide survey

For a regional picture of eurypterid–salt hopper associations, we surveyed all known eurypterid-producing units of Late Ordovician to Early Devonian-age in the Appalachian basin region (i.e., eastern Ohio/southwestern Ontario to easternmost-central New York; northern New York to southwestern West Virginia and western Maryland). We restricted our survey to this region because of the particularly detailed stratigraphic data, often to the bed level, that have been recorded here at multiple localities across a wide geographic range. Collected locality data includes bed-level lithology, presence of microbial structures, and presence of evaporitic structures. These data were collated from field observations, extensive field notes made by one of us in the Appalachian basin (SJC), and the primary literature. For all localities surveyed, the position of the eurypterids within a eurypterid-bearing unit was resolved to the bed level. When multiple localities exposed the same eurypterid-bearing unit, we counted this as a single occurrence. These data, plus taxonomic data, form part of a larger ongoing study of eurypterid *Lagerstätten* preservation in the mid-Paleozoic (Vrazo et al., 2014a).

5. Results of eurypterid–evaporite surveys

5.1. Locality-specific results

In the survey of eurypterids from the Ellicott Creek Breccia Member in the Ciurca Collection, 479 specimens were examined. Virtually all examined specimens were isolated carapaces, with only a handful of partially or nearly fully articulated specimens present. Of those specimens examined, 2% (n = 11) contained either obvious salt hopper structures or evidence for early-stage skeletal halite growth (e.g., Fig. 4). The degree of salt hopper disruption of the specimen depends on the size of the halite crystal, but most hoppers we observed crosscutting eurypterids were small, i.e., <1 cm, compared to the maximum size of isolated hoppers observed in the collection (~5 cm). All observed salt hoppers appeared to be isolated, rather than part of a larger evaporitic raft or mat, and these were generally similar in size and morphology to those that have been previously documented crosscutting eurypterids or other organic material (e.g., Fig. 3A, B). Larger, more developed salt hoppers occur primarily in the middle of a given specimen (i.e., near the center of the carapace) (e.g., Fig. 4A, E–F), whereas incipient evaporite growth seems to occur primarily around carapace margins, resulting in highly disrupted specimens (e.g., Fig. 4A–B). Other than fine (microbial?) laminations, no other identifiable sedimentary or evaporitic structures were found in close association with the examined eurypterid remains. Closely associated fauna were largely absent, with the exception of an occasional putative *Leperditia* impression. It should be noted that most eurypterid-bearing slabs in the Ciurca Collection were cut down to retain only the eurypterid-bearing portion (MBV, personal observation); therefore, it is possible that some specimens were originally found proximal to salt hoppers (i.e., within a few centimeters).

5.2. Region-wide-results

In the survey of all Late Ordovician to Early Devonian-age units in the Appalachian basin, 51 stratigraphic intervals (formation-level or lower) were found to contain eurypterid remains. A majority of these (n = 30) were late Silurian-age, of which 70% (n = 21) occurred within the Bertie Group. A total of 28 surveyed units contained evaporites and 19 (68%) of these contained eurypterids. In other words, 37% (19:51) of all surveyed eurypterid-bearing units contained evaporites (salt hoppers) in the same bed as eurypterid remains (see supplemental data for locality map and stratigraphic occurrences).

The survey results also reveal that the close associations of evaporites and eurypterids are phenomena that are restricted chronostratigraphically to the late Silurian and regionally to the northern basin. With the exception of one occurrence in the Wenlock-age Eramosa Formation (Lockport Group; formerly the Oak Orchard Formation, cf. Ciurca, 1990), all intervals containing both salt hoppers and eurypterids were of late Silurian-age, beginning in the late Ludlovian Vernon Formation and ending in the end-Přídolí–earliest Lochkovian? Honeoye Falls Formation. All formation-level intervals within the Bertie Group of New York and Ontario contain both eurypterids and evaporites in close association, with the exception of the Forge Hollow and Akron Formations, which contain evaporites but no eurypterids. In the subjacent Salina Group, the Syracuse and Vernon Formations show similar eurypterid–salt hopper associations. No eurypterids are known from the subsurface A–F evaporite formations, and eurypterids are completely absent from exposures of the highly evaporitic Camillus Formation.

In the central Appalachian basin (Pennsylvania), late Silurian eurypterids occur in similar carbonate facies (represented by the Tonoloway Formation) as those to the north, but although evaporites are present in some beds here, none closely co-occur with eurypterid remains (Vrazo et al., 2014b). No eurypterid–salt hopper associations are known from the upper Silurian Tonoloway or Wills Creek Formations in the southern Appalachian, despite the prevalence of eurypterids in some beds (Kjellesvig-Waering, 1950; Kjellesvig-Waering and Leutze, 1966; MBV, personal observation).

Evaporite–eurypterid associations in the Appalachian basin appear to be entirely restricted to dolomitic facies, usually massive waterlimes, with the exception of those found in the Vernon Formation, where they occur in thinly laminated black shales. Salt hoppers or early-stage halite molds/casts are the sole evaporitic structure found closely associated with eurypterids. Other evaporitic structures such as relict halite casts/molds or vugs, or chevron halite, were occasionally present in adjacent beds, but none were found on the same bedding plane as eurypterids. Microbial mounds such as stromatolites and thrombolites, or microbially laminated sediments, were the most common sedimentary structure associated with eurypterids. This frequent co-occurrence has been noted previously by Ciurca (e.g., 2013) and will be discussed further elsewhere. Other sedimentary structures (e.g., ripple marks, cross-bedding, bioturbation) in eurypterid-bearing units were rarely observed. Desiccation cracks occur in some intervals, but rarely on the same bedding plane as eurypterids; in the only two examples known, both appear to be the result of post-burial superimposition, rather than contemporaneous formation. Syneresis cracks were absent from examined eurypterid-bearing horizons, although they may be present in adjacent beds.

Some evidence exists for regional variations in salt hopper size and presence within the eurypterid-bearing beds of the Fiddler's Green and Williamsville formations. The coeval ECB and PWM of the Fiddler's Green Formation both contain salt hoppers; however, they are smaller in the ECB of Ontario–western New York compared to the PWM of central New York. The ECB also lacks the desiccation cracks of the latter member. A second, more localized example occurs in the A Member of the Williamsville Formation in western New York and southwestern Ontario. No salt hoppers are known from exposures in Buffalo, New York, and *Lingula* are abundant there, whereas only 22 km to the west at Ridgemount Quarry, Ontario, rare salt hoppers are present and *Lingula* are absent.

Beyond the Appalachian basin to the west, there are a number of eurypterid-bearing units contemporaneous to the Salina and Bertie groups that contain similar dolomitic and/or evaporitic facies, e.g., the Pointe aux Chenes Formation of Michigan, the Bass Islands Group of Ohio and Michigan, the Tymochtee and Greenfield formations of

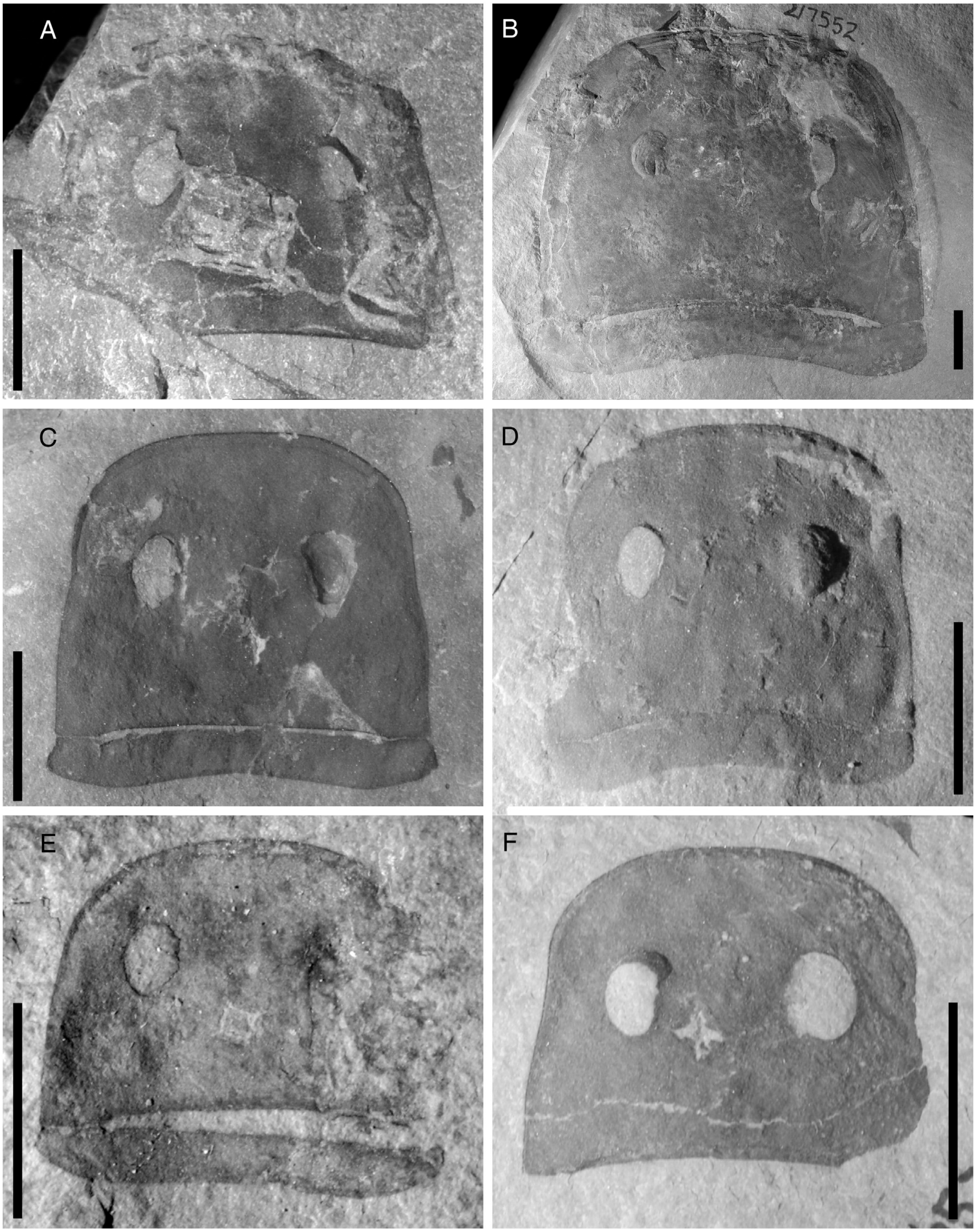

Fig. 4. *Eurypterus* sp. carapaces with disruptive evaporites from the Ellicott Creek Breccia Member (Fiddler's Green Formation), Ridgemount Quarry, Ontario. Scale bars = 1 cm. A) YPM# 214965, with large salt hopper pseudomorph in center and disrupted margins. B) YPM# 217552, with disruptive salt hoppers pseudomorphs near right eye, along margins, and in carapace center. C) YPM# 217513, with early-stage salt hopper/halite pseudomorph in carapace center. D) YPM# 212262, with multiple early-stage salt hopper/halite pseudomorph structures. E) YPM# 214955, with salt hopper pseudomorph in center of carapace and highly disrupted margin on the right side of carapace. F) YPM# 217657, with isolated salt hopper pseudomorph in center of carapace.

Ohio (Landes et al., 1945; Leutze, 1958; Alling and Briggs, 1961; Stumm and Kjellesvig-Waering, 1962), and the Kokomo Limestone Member (Wabash Formation) of Indiana (Clarke and Ruedemann, 1912; Kluessendorf, 1994; Kilibarda and Doff, 2007). However, we are not aware of any documented examples of eurypterids co-occurring with evaporites at the bed level in any of these intervals. If the survey is extended to include all Laurentian eurypterid occurrences, the earliest (and only additional) example of a close eurypterid–halite evaporite association on the same bedding plane is found in the Upper Ordovician Stony Mountain Formation of Manitoba (Young et al., 2007; G.A. Young, personal communication, 2014), which has been interpreted as having a Bertie-like depositional environment.

6. Discussion

Salt hoppers in eurypterid-bearing units in the Salina and Bertie groups appear to be predominantly displacive, i.e., they completed development on the sediment surface, or interstitially within supersaturated subsurface sediments, rather than at the air-water interface or in the water column in bodies of brine as in the model proposed by Dellwig (1955) and others. This type growth is supported by the observation that many salt hopper structures crosscut laminated sediments and biogenic substrates (i.e., thrombolites; Fig. 3C), and the presence of evaporitic dendrites, which cut through the surrounding and presumably uncompacted matrix (Fig. 2A–B). Such crosscutting indicates that development of the hopper structure was completed only following deposition of the surrounding sediments or biogenic material. Growth either on or in the sediment is further supported by the large size of many hoppers, which were probably not capable of remaining buoyed at the air-water interface, or in the water column, based on experimental results (cf. Dellwig, 1955; Arthurton, 1973) (e.g., Fig. 2C–E). A critical question is whether salt hoppers associated with eurypterids began their initial growth at the air-water interface and completed development on or in the sediment surface, or began and completed their growth entirely within the sediment. The following lines of evidence suggests the latter: neither relict halite raft structures (suggestive of buoyed crystal growth on the brine surface; Dellwig, 1955; Shearman, 1970; Arthurton, 1973), nor syntaxial crystal overgrowths (suggestive of halite growth on the sediment surface; Dellwig, 1955; Lowenstein and Hardie, 1985), have been observed in eurypterid-bearing beds. Furthermore, the regular confinement of salt hoppers or their incipient forms to within the specimen periphery, rather than adjacent to them, suggests to us that growth of these structures may have only commenced following deposition of the specimen on or in the substrate; i.e., eurypterids and other organic structures might have acted as nucleation points for halite development following burial. Considering the available evidence, it seems plausible that salt hopper growth in eurypterid-bearing beds largely occurred within the sediment, rather than in the water column, and only after burial of the eurypterids themselves. In turn, it can be inferred that salt hopper formation and burial of eurypterid remains were not concurrent events. But were the eurypterids themselves buried under hypersaline conditions?

The pervasiveness of salt hoppers, gypsum molds, and other evaporitic structures in the dolomitic units of the upper Silurian Appalachian basin suggests that this region was particularly prone to evaporite deposition. Primary or pencontemporaneous dolomite is the first evaporite to precipitate out of solution when salinity rises above ~70 ppt (Scruton, 1953). In the context of the circulation restricted and arid Appalachian basin, it is plausible that the water column regularly became saturated in $CaCO_3$ and Mg, leading to the deposition of evaporitic primary dolomite, or post-depositional penecontemporaneous dolomite. Halite evaporites only occur at salinity levels at ~350 ppt and above and, thus, under this evaporitic regime, the prevalence of salt hoppers within dolomitic units containing eurypterids and other fauna would seem to indicate that their deposition took place under extremely hypersaline–briny conditions. In the Bertie Group, primary or penecontemporaneous dolomites have been interpreted in some eurypterid-bearing intervals, such as in the Phelps Waterlime Member (Andrews et al., 1974). Although, early post-depositional or penecontemporaneous dolomite cannot be ruled out, two pieces of evidence suggest that dolomite precipitation was probably not syndepositional with organism burial. Firstly, a diverse fauna that includes fish is found in one of the most prolific eurypterid-bearing waterlimes, the A Member of the Williamsville Formation (Burrow and Rudkin, 2014; Ciurca, personal observation). This indicates that salinity conditions at the time of deposition were probably near normal marine or hyposaline. Belak (1980) noted a similarly stenohaline and subtidal fauna in certain dolomites of the suprajacent Cobleskill and Akron Formations and suggested that this negated the possibility of pencontemporaneous dolomitization in those intervals. Belak suggested instead that magnesium-rich brines saturated the limestones in the intertidal–supratidal zones of the Cobleskill and Akron shoreface following sea level regression. Secondly, formation of penecontemporaneous dolomite following organism burial, or even secondary dolomitization of sediments throughout upper Silurian units in the Appalachian basin is supported by fossil alteration. Skeletons of mineralized organisms (e.g., gastropods, cephalopods, bivalves, and brachiopods) found in waterlimes and calcareous shales from the Bertie Group and coeval intervals (e.g., the Tonoloway Formation) are usually represented by molds or as infilled voids, suggesting diagenetic alteration. If we conclude that the eurypterid-bearing waterlimes of the Bertie Group were most likely not precipitated as primary dolomitic sediments under evaporative conditions at the air-water interface, this suggests that the interbedded evaporites may have also formed under a different evaporitic regime.

6.1. Model for intrasedimentary salt hopper development

The proposed intrasedimentary formation of disruptive salt hoppers in the upper Silurian Salina and Bertie groups described above requires a developmental pathway dependent primarily on NaCl-saturated groundwater, rather than surface brines. In their description of displacive salt hoppers in sub-Recent Dead Sea sediments, Gornitz and Schreiber (1981) proffered two possible pathways for intrasedimentary salt hopper growth in a muddy substrate. Concentrated brines either: a) diffused downward into submerged sediments from the water column, or b) diffused upward though the interstitial space of the capillary fringe following vadose zone exposure to air. Both pathways allow for development of hopper-shaped halite crystals in the sediment, but differ in terms of evaporation taking place over subaqueous or subaerially exposed sediments, respectively. Eurypterids in the Salina and Bertie groups regularly occur within cyclic, shallowing-upward successions whose uppermost beds show evidence for subaerial exposure (e.g., the extensive desiccation cracks of the PWM), but lack evaporites. Thus, in considering Gornitz and Schreiber's pathways for intrasedimentary salt hopper formation, it seems more likely that salt hoppers in these units were formed via upward diffusion of brines during a regressive phase, whereby saturated fluids laterally permeated the subsurface as evaporation drove upward migration of the brines through capillary space of air-exposed sediment in the vadose zone. However, we cannot rule out that salt hoppers and other evaporites in some units may have formed via downward diffusion of supersaturated brines into the sediment from shallow evaporitic pools. This latter pathway may explain the barren dissolution breccia in the uppermost beds of the ECB, for example.

Basin topography also supports this proposed sequence of events leading to close eurypterid–salt hopper associations. The slope of the carbonate ramp in the late Silurian Appalachian basin was extremely gentle (Belak, 1980; Bell and Smosna, 1999) and during regressive phases, sea level and the height of the water table would have shifted in elevation very gradually along the shallow slope. This would have created prolonged periods of surface and groundwater stagnation in the intertidal–supratidal vadose and phreatic zones, respectively. In conjunction with regression, surface evaporation due to the arid climate and a lack of regular oceanic input would have quickly elevated salinity levels in the basin margin to the point of supersaturation. As the intertidal–supratidal zones became increasingly subaerially exposed and groundwater became briny, halite crystals in the subsurface may have preferentially nucleated on buried organic material such as eurypterid cuticle, leading to the intimate salt hopper-eurypterid relationship we have documented above (Fig. 5).

This regressive pathway for hopper formation may also explain why hoppers are found on multiple horizons within single beds—as sea level dropped, the phreatic zone would have shifted, creating multiple nucleation horizons—as well as the size/abundance variations noted in some intervals. In a study of a sub-Recent playa basin, Handford (1982) noted that the greatest intrasedimentary hopper growth occurred in the subaerial saline mudflat stage, and that salt hopper size appears to reflect growth rates. In considering similar mudflat-sabkha-type settings on the margins of the Appalachian basin (e.g., Smosna et al., 1977; Belak, 1980; Hamell and Ciurca, 1982), the large size of salt hoppers in some units such as the PWM in central New York may reflect a slow rate of regression and prolonged development in a subaerially exposed sediment, whereas the smaller hoppers in the ECB to the west may reflect slightly deeper subaqueous conditions. Similarly, the presence of salt hoppers in the Williamsville Formation A Member of southwestern Ontario, and their absence (and the presence of *Lingula*) in Buffalo, New York, seems to suggest the formation of a steep east–west halocline following eurypterid deposition; from hypersaline, to normal marine or even hyposaline, respectively.

6.2. Implications for eurypterid paleoecology

If our model is valid, this strongly calls into question the hypothesis that eurypterids actively occupied the penesaline or extremely hypersaline conditions of the late Silurian, and reinforces our view that eurypterids preserved in these carbonate ramp settings were primarily denizens of subtidal settings with near normal marine conditions (i.e., from hyposaline to slightly hypersaline). However, if eurypterids avoided the most extreme nearshore settings, this raises a simple but lingering question; Where did eurypterids go when conditions became briny? Appalachian basin paleogeography suggests that eurypterids moved either inland via estuaries or deltas to the east, or into more normal marine conditions to the south. For eurypterids in the “Salina Series” (i.e., most of what is now the Salina and Bertie groups), Clarke and Ruedemann (1912) postulated the former, essentially suggesting that this predicated the predominantly freshwater habitat of later Devonian eurypterids (but see O'Connell, 1916, for a counterargument). Early Silurian eurypterid remains from the coeval Tuscarora and Shawangunk Formations of Pennsylvania and New York, respectively (Smith, 1970; Cotter, 1983), occur in thin dark shales interbedded within massive conglomeratic arenites (Clarke and Ruedemann, 1912; MBV, personal observation) and may represent such inland incursions. Although there is no firm agreement on the depositional environment of these intervals—they were most likely deposited in either a fluvial or estuarine-type deposit, or within a marine-influenced but low-energy back-bar-type setting (Epstein, 1993)—they almost certainly were not hypersaline.

Alternatively, if eurypterids ventured into more fully marine settings, the late Silurian Keyser Formation of Pennsylvania, Maryland, and West Virginia represents a likely depositional environment. The Keyser Formation appears to be contemporaneous with the uppermost Bertie Group and largely represents a subtidal and normal marine reef environment (Makurath, 1977). This interval also contains intermittent carbonate facies similar to those that contain eurypterids in the Bertie Group, although these have not yet yielded eurypterids. Unequivocal evidence for marine occupation of normal marine environments similar to the Keyser Formation comes from the diverse early Silurian

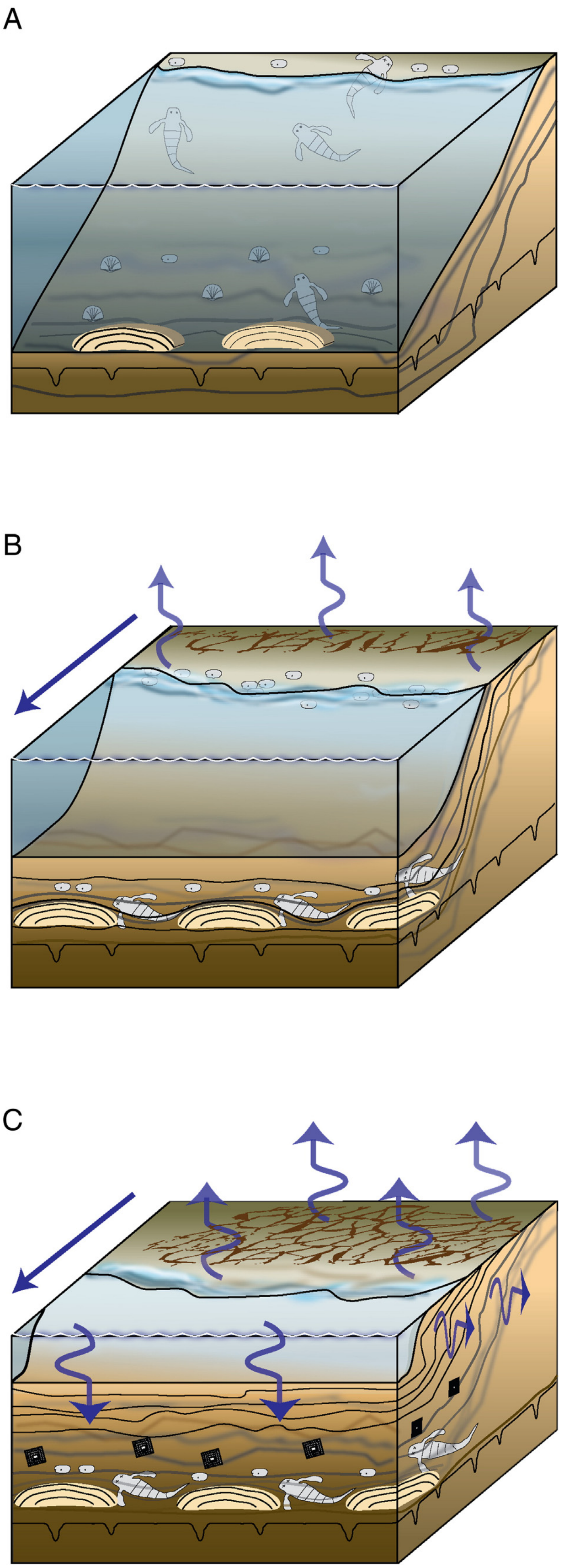

Fig. 5. Cartoon model of generalized depositional environment succession leading to salt hopper development in eurypterid-bearing units in the Appalachian basin. Not to scale. A) Subtidal environment, following transgression. Eurypterids and limited marine fauna are present, as are stromatolites/thrombolites. B) Generalized intertidal–supratidal environment, following regression. Evaporation (wavy arrows) begins to produce desiccation cracks. Eurypterids are absent and remains are buried. Only tolerant euryhaline organisms (e.g., leperditicopids) are present as conditions become increasingly hypersaline and/or dysoxic. C) Supratidal–sabkha-like environment. Continuing regression and evaporation creates in hypersaline conditions and units are barren. Supersaturation of groundwater with NaCl leads to *in situ* salt hopper formation in the sub-surface. Eurypterids and microbial material appear to act as nucleation points (see Fig. 3 for examples).

(Llandovery) death assemblage of the Pentland Hills *Lagerstätte* in Scotland where eurypterids, including *Eurypterus*?, are found with euhaline taxa, including a variety of echinoderms (Lamsdell, 2011).

6.3. Eurypterid preservation

In our model of interstitial salt hopper formation in eurypterid-bearing units, we envisage eurypterid burial and salt hopper development as temporally separate and sequential events; salt hopper formation only occurred following burial of eurypterids and contemporaneous fauna. This temporal gap between eurypterid burial and evaporite formation would preclude their preservation in Leutze's (1961) "pickling brine"—although if evaporitic brines began percolating downward within a few centuries after eurypterid burial, they may have aided in long-term preservation. If any evidence for *in situ* eurypterid pickling exists, it may come from the Upper Devonian Osovets beds of the Starobin potassium-salt basin in Belarus where several stylonurid specimens have been collected from thin clay bands interbedded within thick sylvinite deposits (Plax and Barbikov, 2009).

Slight to moderate (sub-evaporitic) hypersalinity in the water column, on the other hand, may have played a more immediate, if less evident role in eurypterid preservation. Increases in temperature and salinity reduce aquatic oxygen concentrations (Warren, 2006). Evaporation in the Appalachian basin would have been capable of driving salinity to beyond habitable levels and establishing concomitant dysoxic or anoxic conditions that typically exclude bioturbators and biodegraders (e.g., Fig. 5B). In this stagnant environment, the likelihood of eurypterid cuticle and other soft-tissue organism (e.g., early plants, worms) preservation would increase (Kluessendorf, 1994; Edwards et al., 2004; SJC, personal observation). This combination of hypersaline brines and anoxia as a preservational agent for arthropod cuticle has been cited elsewhere in Recent (Mutel et al., 2008; Parsons-Hubbard et al., 2008) and ancient aquatic environments (Barthel et al., 1990).

Beyond the Appalachian basin, within Laurentia and elsewhere, our depositional model is likely to be applicable to other carbonate ramp settings in which eurypterid faunas occur in nearshore dolomitic and evaporitic facies. For example, in the Bertie-like Late Ordovician Stony Mountain Formation *Lagerstätte* in Manitoba, Canada, G.A. Young (personal communication, 2015) has suggested that halite associated with eurypterids may have formed post-burial. Similarly, in the Silurian of Baltica and the Ukraine, where a eurypterid fauna comparable to that of the Bertie Group is found in a similar depositional environment (Viira and Einasto, 2003; Meidla et al., 2014; SJC, personal observation), preservation probably occurred in a similar manner.

7. Conclusions

Past interpretations of eurypterid habitats in the late Silurian Appalachian basin were often a byproduct of inferred depositional environment at coarse stratigraphic scales. Lumping of eurypterid-bearing units with barren, evaporitic deposits led to generalizations regarding paleosalinity and eurypterid halotolerance. The frequently restricted fauna of the Salina and Bertie groups has also informed such interpretations of paleoenvironment, although we question the utility of these faunas for interpretations of paleosalinity in the absence of sedimentary evidence. More recently it has become clear that a full understanding of eurypterid paleoecology and preservation in the Appalachian basin and elsewhere can only occur within a revised stratigraphic framework (Brett et al., 1990; Ciurca, 1990).

From the survey results and the sequence of events in our proposed model, we can make three broad conclusions: firstly, the margins of the Appalachian basin during the late Silurian were frequently hypersaline, thus reaffirming the long-held view of the regional paleoenvironment at this time; secondly, and more importantly, the association of eurypterids and salt hoppers appears to be the result of early-stage diagenetic overprinting following deposition, rather than a reflection of conditions in the eurypterid life habitat; thirdly, eurypterid remains probably reflect burial in very shallow subtidal deposits, rather than transport into intertidal–supratidal settings. From these conclusions, we are able to refute to a large degree the traditional notion that eurypterids occupied hypersaline conditions during the late Silurian. This is significant when considering eurypterid paleoecology and evolution—constraining the likely eurypterid habitat in the Appalachian basin to near normal marine or hyposaline subtidal settings represents a critical step toward a better understanding of eurypterid environmental preferences during a transitional time in their history.

Acknowledgments

The authors would like to thank Susan Butts and Jessica Utrup (Yale Peabody Museum) for their collections assistance. Timothy Phillips is thanked for assistance with figure drafting. We gratefully acknowledge Stephen Bell, Ray Garton, Trent Spielman, and Jeffrey Trop for field assistance, specimen collection, and locality discussion. We thank Graham Young and Peter Van Roy for their helpful suggestions and thoughtful reviews of this manuscript. This study was supported by grants to MBV from the University Of Cincinnati Chapter Of Sigma Xi, the Geological Society of America, the Schuchert and Dunbar Grant-in-Aid Program (Yale Peabody Museum), and the Caster Fund (University of Cincinnati), and the University of Cincinnati Graduate School Dean's Fellowship.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.palaeo.2015.12.011. These data include the google map of the most important areas described in this article.

References

Alling, H.A., Briggs, L.I., 1961. Stratigraphy of upper Silurian Cayugan evaporites. AAPG Bull. 45, 515–547.

Andrews, H.E., Brower, J.C., Gould, S.J., Reyment, R.A., 1974. Growth and variation in *Eurypterus remipes* DeKay. Bulletin of the Geological Institution of the University of Uppsala. New Ser. 4, 81–114.

Arthurton, R.S., 1973. Experimentally produced halite compared with Triassic layered halite-rock from Cheshire, England. Sedimentology 20, 145–160.

Barthel, K.W., Swinburne, N.H.M., Conway Morris, S., 1990. Solnhofen: A Study in Mesozoic Palaeontology. Cambridge University Press, New York.

Belak, R., 1980. The Cobleskill and Akron members of the Rondout Formation: late Silurian carbonate shelf sedimentation in the Appalachian basin, New York State. J. Sediment. Res. 50, 1187–1204.

Bell, S.C., Smosna, R., 1999. Regional facies analysis and carbonate ramp development in the Tonoloway Limestone (upper Silurian; central Appalachians). Southeast. Geol. 38, 259–278.

Braddy, S.J., 2001. Eurypterid palaeoecology: palaeobiological, ichnological and comparative evidence for a 'mass-moult-mate' hypothesis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 172, 115–132.

Brett, C.E., Goodman, W.M., LoDuca, S.T., 1990. Sequences, cycles, and basin dynamics in the Silurian of the Appalachian foreland basin. Sediment. Geol. 69, 191–244.

Burrow, C.J., Rudkin, D., 2014. Oldest near-complete acanthodian: the first vertebrate from the Silurian Bertie Formation Konservat-Lagerstätte, Ontario. PLoS ONE 9, 1–9.

Ciurca Jr., S.J., 1973. Eurypterid horizons and the stratigraphy of upper Silurian and Lower Devonian rocks of western New York State, New York State Geological Association, 45th Annual Meeting. Brockport, New York, pp. D1–D14.

Ciurca Jr., S.J., 1990. Eurypterid biofacies of the Silurian–Devonian evaporite sequence: Niagara Penninsula, Ontario, Canada and New York State. In: Lash, G.G. (Ed.), New York State Geological Association, 62nd Annual Meeting. Fredonia, New York, pp. D1–D23.

Ciurca Jr., S.J., 2005. Eurypterids and facies changes within the Silurian/Devonian "Eurypterid Beds" of New York State. In: Valentino, D.W. (Ed.), New York State Geological Association, 77th Annual Meeting, Albany, New York, pp. 113–121.

Ciurca Jr., S.J., 2010. Eurypterids Illustrated: The Search for Prehistoric Sea Scorpions. PaleoResearch, Rochester, New York.

Ciurca Jr., S.J., 2011. Silurian and Devonian eurypterid horizons in upstate New York. In: Nelson, N. (Ed.), New York State Geological Association, 83rd Annual Meeting, Syracuse, New York, pp. 139–151.

Ciurca Jr., S.J., 2013. Microbialites within the eurypterid-bearing Bertie Group of western New York and Ontario, Canada. In: Baird, G., Wilson, M. (Eds.), New York State Geological Association, 85th Annual Meeting, Fredonia, New York, pp. 154–179.

Ciurca Jr., S.J., Hamell, R.D., 1994. Late Silurian sedimentation, sedimentary structures and paleoenvironmental settings within an eurypterid-bearing sequence (Salina and Bertie groups), Western New York State and Southwestern Ontario, Canada. In: Brett, C.E., Scatterday, J. (Eds.), New York State Geological Association, 66th Annual Meeting. Rochester, New York, pp. 457–488.

Clarke, J.M., 1907. The *Eurypterus* shales of the Shawangunk mountains in eastern New York. N. Y. State Mus. Bull. 107, 295–310.

Clarke, J.M., Ruedemann, R., 1912. The Eurypterida of New York. N. Y. State Mus. Mem. 14, 1–439.

Cotter, E.C., 1983. Shelf, paralic, and fluvial environments and eustatic sea-level fluctuations in the origin of the Tuscarora Formation (lower Silurian) of central Pennsylvania. J. Sediment. Petrol. 53, 25–49.

Dellwig, L.F., 1955. Origin of the Salina salt of Michigan. J. Sediment. Res. 25, 83–110.

Dennison, J.M., Head, J.W., 1975. Sealevel variations interpreted from the Appalachian basin Silurian and Devonian. Am. J. Sci. 275, 1089–1120.

Edwards, D., Banks, H.P., Ciurca, S.J., Laub, R.S., 2004. New Silurian cooksonias from dolostones of north-eastern North America. Bot. J. Linn. Soc. 146, 399–413.

Ehlinger, G.S., Tankersley, R.A., 2004. Survival and development of horseshoe crab (*Limulus polyphemus*) embryos and larvae in hypersaline conditions. Biol. Bull. 206, 87–94.

Epstein, J.B., 1993. Stratigraphy of Silurian rocks in Shawangunk Mountain, southeastern New York, including a historical review of nomenclature. U.S. Geol. Surv. Bull. 1839, L1–L38.

Gornitz, V.M., Schreiber, B.C., 1981. Displacive halite hoppers from the Dead Sea: some implications for ancient evaporite deposits. J. Sediment. Res. 51, 787–794.

Hamell, R.D., 1982. Stratigraphy, petrology, and paleoenvironemntal interpretation of the Bertie Group (Late Cayugan) in New York. Emp. State Geogram 18, 37–38.

Hamell, R.D., Ciurca Jr., S.J., 1982. Paleoenvironmental analysis of the Fiddlers Green Formation (late Silurian) in New York State, New York State Geological Association, 58th Annual Meeting, Ithaca, New York. pp. 199–218.

Handford, C.R., 1982. Sedimentology and evaporite genesis in a Holocene continental-sabkha playa basin-Bristol Dry Lake, California. Sedimentology 29, 239–253.

Hartnagel, C.A., 1903. Preliminary observations on the Cobleskill ("coralline") limestone of New York. N. Y. State Mus. Bull. 69, 1109–1175.

Kaneshiro, E.S., 1962. Growth patterns in *Eurypterus remipes remipes* DeKay 1825 Unpublished M.S. Thesis Department of Geology, Syracuse University, Syracuse, New York, p. 37.

Kilibarda, Z., Doff, J., 2007. Mudcracks, bird's-eye, and anhydrite in intertidal/supratidal late Silurian Kokomo Limestone, Indiana. Proc. Indiana Acad. Sci. 16, 1–10.

Kjellesvig-Waering, E.N., 1950. A new Silurian *Hughmilleria* from West Virginia. J. Paleontol. 24, 226–228.

Kjellesvig-Waering, E.N., 1958. The genera, species and subspecies of the family Eurypteridae, Burmeister, 1845. J. Paleontol. 32, 1107–1148.

Kjellesvig-Waering, E.N., 1961. The Silurian Eurypterida of the Welsh Borderland. J. Paleontol. 35, 789–835.

Kjellesvig-Waering, E.N., 1966. Silurian scorpions of New York. J. Paleontol. 40, 359–375.

Kjellesvig-Waering, E.N., Leutze, W.P., 1966. Eurypterids from the Silurian of West Virginia. J. Paleontol. 40, 1109–1122.

Kluessendorf, J., 1994. Predictability of Silurian Fossil-Konservat-Lagerstätten in North America. Lethaia 27, 337–344.

Lamsdell, J.C., 2011. The eurypterid *Stoermeropterus conicus* from the lower Silurian of the Pentland Hills, Scotland. Monogr. Palaeontograph. Soc. 165, 1–84 pls 81–15.

Lamsdell, J.C., Braddy, S.J., 2010. Cope's Rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. Biol. Lett. 6, 265–269.

Lamsdell, J.C., Braddy, S.J., Tetlie, O.E., 2009. Redescription of *Drepanopterus abonensis* (Chelicerata: Eurypterida: Stylonurina) from the Late Devonian of Portishead, UK. Palaeontology 52, 1113–1139.

Landes, K.K., Ehlers, G.E., Stanley, G.M., 1945. Geology of the Mackinac Straits region. Michigan Geological Survey Publication 44. Geological Series 37.

Leitner, C., Neubauer, F., Marschallinger, R., Genser, J., Bernroider, M., 2013. Origin of deformed halite hopper crystals, pseudomorphic anhydrite cubes and polyhalite in Alpine evaporites (Austria, Germany). Int. J. Earth Sci. 102, 813–829.

Leutze, W.P., 1958. Eurypterids from the Silurian Tymochtee dolomite of Ohio. J. Paleontol. 32, 937–942.

Leutze, W.P., 1961. Arthropods from the Syracuse Formation, Silurian of New York. J. Paleontol. 49–64.

Lowenstein, T.K., Hardie, L.A., 1985. Criteria for the recognition of salt-pan evaporites. Sedimentology 32, 627–644.

Makurath, J.H., 1977. Marine faunal assemblages in the Silurian–Devonian Keyser Limestone of the central Appalachians. Lethaia 10, 235–256.

McKenzie, S.C., 2014. First fishes from the Silurian (Pridolian) Bertie *Lagerstätte* of New York State, Geological Society of America, Northeastern Section, 49th Annual Meeting. Lancaster, PA.

Meidla, T., Tinn, O., Männik, P., 2014. Stop B8: Soeginina cliff. In: Bauert, H., Hints, O., Meidla, T., Männik, P. (Eds.), 4th Annual Meeting of IGCP 591, Estonia, 10–19 June 2014Abstracts and Field Guide. University of Tartu, Tartu, Tartu, Estonia, pp. 194–196.

Mutel, M.H.E., Waugh, D.A., Feldmann, R.M., Parsons-Hubbard, K.M., 2008. Experimental taphonomy of *Callinectes sapidus* and cuticular controls on preservation. Palaios 23, 615–623.

Nolan, P.R., 2014. A reappraisal of flora in the Bertie Group and their potential significance in analyzing the environment of late Silurian New York State and Canada, Geological Society of America, Northeastern Section, 49th Annual Meeting. Lancaster, PA.

O'Connell, M., 1916. The habitat of the Eurypterida. Bull. Buffalo Soc. Nat. Sci. 11, 1–227.

Parsons-Hubbard, K.M., Powell, E.N., Raymond, A., Walker, S.E., Brett, C.E., Ashton-Alcox, K., Shepard, R.N., Krause, R., Deline, B., 2008. The taphonomic signature of a brine seep and the potential for Burgess Shale style preservation. J. Shellfish Res. 27, 227–239.

Plax, D.P., Barbikov, D.V., 2009. Eurypterid (Chelicerata, Eurypterida) findings in Famennian saliniferous deposits of the Devonian of Belarus. Lithosphere 1, 29–38.

Plotnick, R.E., 1999. Habitat of Llandoverian–Lochkovian eurypterids. In: Boucot, A.J., Lawson, J.D. (Eds.), Paleocommunities, A Case Study from the Silurian and Lower Devonian. Cambridge University Press, Cambridge, pp. 106–131.

Rickard, L.V., 1969. Stratigraphy of the upper Silurian Salina Group: New York, Pennsylvania, Ohio, Ontario. New York State Museum and Science Service. Geological Survery Map and Chart series no. 12, Albany, NY.

Ruedemann, R., 1925. The Bertie Waterlime fauna, in some Silurian (Ontarian) faunas of New York. N.Y. State Mus. Bull. 265, 8–14.

Sarle, C.J., 1903. A new eurypterid fauna from the base of the Salina of western New York. N.Y. State Mus. Bull. 69, 1080–1108.

Scruton, P.C., 1953. Deposition of evaporites. AAPG Bull. 37, 2498–2512.

Selden, P.A., 1984. Autecology of Silurian eurypterids. In: Bassett, M.G., Lawson, J.D. (Eds.), Autecology of Silurian organismsSpecial Papers in Palaeontology. The Palaeontological Association, pp. 39–54.

Shearman, D.J., 1970. Recent halite rock, Baja California, Mexico. Transactions of the Institution of Mining and Metallurgy, Section B: Applied Earth Science 79, 155–162.

Shearman, D.J., 1978. Halite in sabkha environments. In: Dean, W.E., Schreiber, B.C. (Eds.), Marine Evaporites. SEPM, Tulsa, Arizona, pp. 430–442.

Shuster, C.N., 1982. A pictoral review of the natural history and ecology of the horseshoe crab *Limulus polyphemus* with reference to other Limulidae. Physiology and biology of horseshoe crabs. Studies on normal and environmentally stressed animals 81, pp. 1–52.

Sloss, L.L., 1969. Evaporite deposition in mixed solutions. AAPG Bull. 53, 776–789.

Smith, N.D., 1970. The braided stream depositional environment: comparison of the Platte River with some Silurian clastic rocks, north-central Appalachians. Geol. Soc. Am. Bull. 81, 2993–3014.

Smosna, R., Patchen, D., Warshauer, S., Perry, J.W., 1977. Relationships between depositional environments, Tonoloway Limestone, and distribution of evaporites in the Salina Formation, West Virginia, SG 5: reefs and evaporites—concepts and depositional models. Am. Assoc. Pet. Geol. 125–143.

Southgate, P.N., 1982. Cambrian skeletal halite crystals and experimental analogues. Sedimentology 29, 391–407.

Størmer, L., 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. Senckenb. Lethaea 57, 87–183.

Stumm, E.C., Kjellesvig-Waering, E.N., 1962. A new eurypterid from the upper Silurian of southern Michigan. Contrib. Mus. Paleontol. 17, 195–204.

Tetlie, O.E., 2006. Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus. J. Syst. Palaeontol. 4, 397–412.

Tetlie, O.E., 2007. Distribution and dispersal history of Eurypterida (Chelicerata). Palaeogeogr. Palaeoclimatol. Palaeoecol. 252, 557–574.

Tetlie, O.E., Brandt, D.S., Briggs, D.E.G., 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). Palaeogeogr. Palaeoclimatol. Palaeoecol. 265, 182–194.

Tollerton Jr., V.P., 1997. Eurypterids and associated fauna at Litchfield, a classic locality. In: Rayne, T.W., Bailey, D.G., Tewksbury, B.J. (Eds.), New York State Geological Association, 69th Annual Meeting. Clinton, New York, pp. 253–264.

Tollerton Jr., V.P., Muskatt, H.S., 1984. Sedimentary structures and paleoenvironmental analysis of the Bertie Formation (upper Silurian, Cayugan Series) of central New York State. In: Brett, C.E., Scatterday, J. (Eds.), New York State Geological Association, 56th Annual Meeting, Clinton, NY, pp. 117–155.

Tourek, T.J., 1970. The depositional environments and sediment accumulation models for the upper Silurian Wills Creek shale and Tonoloway limestone, central Appalachians Unpublished Ph.D. Dissertation Johns Hopkins University, Baltimore, Maryland, p. 564.

Van der Voo, R., 1988. Paleozoic paleogeography of North America, Gondwana, and intervening displaced terranes: comparisons of paleomagnetism with paleoclimatology and biogeographical patterns. Geol. Soc. Am. Bull. 100, 11–324.

Vannier, J., Wang, S.Q., Coen, M., 2001. Leperditicopid arthropods (Ordovician–Late Devonian): functional morphology and ecological range. J. Paleontol. 75, 75–95.

Viira, V., Einasto, R., 2003. Wenlock–Ludlow boundary beds and conodonts of Saaremaa Island, Estonia. Proceedings of the Estonian Academy of Sciences. Geology 52, 213–238.

Vrazo, M.B., Braddy, S.J., 2011. Testing the 'mass-moult-mate' hypothesis of eurypterid palaeoecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 311, 63–73.

Vrazo, M.B., Ciurca Jr., S.J., Brett, C.E., 2014a. Taphonomic and ecological controls on eurypterid Lagerstätten: a model for preservation in the mid-Paleozoic. Geol. Soc. Am. Abstr. Programs 46, 578.

Vrazo, M.B., Trop, J.M., Brett, C.E., 2014b. A new eurypterid Lagerstätte from the upper Silurian of Pennsylvania. Palaios 29, 431–448.

Warren, J.K., 2006. Evaporites: sediments. Resources and Hydrocarbons. Springer Berlin, Heidelberg.

Warshauer, S.M., Smosna, R., 1977. Paleoecologic controls of the ostracode communities in the Tonoloway Limestone (Silurian; Pridoli) of the central Appalachians. In: Loffler, H., Danielopol, D. (Eds.), Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda. W. Junk, The Hague, pp. 475–485.

Waterston, C.D., 1979. Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea. Transactions of the Royal Society of Edinburgh. Earth Sci. 70, 251–322.

Young, G.A., Rudkin, D.M., Dobrzanski, E.P., Robson, S.P., Nowlan, G.S., 2007. Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. Geology 35, 883–886.