



## Testing the ‘mass-moult-mate’ hypothesis of eurypterid palaeoecology

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### ABSTRACT

The eurypterids (Arthropoda: Chelicerata), some of the earliest arthropods to undertake amphibious excursions onto land, are generally rare in the fossil record, but are sometimes found in great abundance, for example in the Late Silurian Bertie Group of New York State. The mass-moult-mate hypothesis has been proposed to explain such occurrences, whereby eurypterids undertook mass migrations into near shore settings and lagoons to moult, mate and spawn, similar to the behaviour of living horseshoe crabs. This hypothesis is tested using measurements from over 600 *Eurypterus* specimens from three localities in the Bertie Group; *Eurypterus remipes*, from the Fiddlers Green Formation, and the slightly larger *Eurypterus lacustris*, from the overlying Williamsville Formation. Disarticulation patterns support previous evidence for moulted assemblages. A significant predominance of female exuviae is noted at each locality, unlike studies on modern *Limulus* populations. Therefore, a modified mass-mate-spawn-moult hypothesis is proposed here: males returned to deeper waters after mating, whereas females, having mated, remained at the breeding sites to deposit their eggs before moulting. After hatching, eurypterid larvae and juveniles remained in these spawning grounds until they matured and could move to deeper water, in comparison with *Limulus*. This hypothesis is also discussed in light of recent work on the gender determination of the type ‘A’ and type ‘B’ genital appendages.

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### 1. Introduction

The eurypterids were Palaeozoic aquatic chelicerates that attained their peak diversity in the Silurian and Early Devonian (Plotnick, 1999). They originated in marine environments, were some of the earliest arthropods to undertake amphibious excursions onto land (Braddy, 2001), and were gradually confined to entirely freshwater habitats by the Carboniferous (Plotnick, 1999). Eurypterids are more derived than horseshoe crabs (Xiphosura), and sister group to scorpions (see Dunlop and Selden, 1997; Dunlop and Braddy, 2001, for discussion), yet both these living groups provide useful modern analogues for different aspects of eurypterid palaeobiology, behaviour and ecology (e.g. Andrews et al., 1974; Braddy, 2001; Tetlie et al., 2008), and taphonomy (McCoy and Brandt, 2009).

Although generally rare in the fossil record, abundant accumulations of eurypterids, often articulated and well preserved *Eurypterus* spp., are known from a few Late Silurian localities, most notably in the Bertie Group that outcrops in New York State, USA and Ontario, Canada (Braddy, 2001). The reason for such localised abundance remains unclear, although a mass-moult-mate hypothesis (Braddy, 2001), offers a potential explanation: eurypterids undertook excursions into lagoons and other marginal settings to moult, mate and

spawn *en masse*, a behaviour that is suggested in other ancient groups (e.g. trilobites [Speyer and Brett, 1985; Karim and Westrop, 2002] and euthycarcinoids [MacNaughton et al., 2002]), and modern horseshoe crabs (Rudloe, 1980).

Based on the distribution results from moult assemblages of other eurypterids (e.g. Kues and Kietzke, 1981) and related marine arthropods (e.g. trilobites [Speyer and Brett, 1985; Karim and Westrop, 2002]), and gender biases seen at the breeding grounds of modern xiphosurans (e.g. Rudloe, 1980; Carmichael et al., 2003), we would expect the following *a priori* results to support the hypothesis that the Bertie Group was both a site of mass-moulting and mating by eurypterids: a) a non-normal, bimodal population distribution with predominance of larval and adult stages; b) gender bias towards males, and c) patterns of disarticulation indicating proximity to a moulting site.

This study therefore aims to empirically test the mass-moult-mate hypothesis via a large-scale analysis of *Eurypterus* specimens from three site-specific sample populations from the Bertie Group of New York State and Ontario. The size and gender distributions of putative species *Eurypterus remipes* DeKay, 1825 and *Eurypterus lacustris* Harlan, 1834 are analysed, as are patterns of disarticulation.

### 2. Historical review

Previous research has investigated general patterns in eurypterid ecology (e.g. Plotnick, 1999; Braddy, 2001). This historical review is

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therefore confined to the mass-moult-mate hypothesis (Braddy, 2001), the inter-specific variation between *E. remipes* and *E. lacustris* and the geological, ecological and taphonomic context of the Bertie Group eurypterid assemblage.

### 2.1. The mass-moult-mate hypothesis

The palaeobiology of eurypterids indicates that they were capable of brief amphibious excursions onto land, a useful adaptation were they travelling into shallow, occasionally arenaceous environments to mate and moult. At least some eurypterids, e.g. *Eurypterus*, possessed both book-gills, for aquatic respiration, and Kiemenplatten, for aerial respiration during short periods (Selden, 1985; Manning and Dunlop, 1995; Braddy et al., 1999). The Kiemenplatten enabled them to migrate across marginal, sub-aerial settings *en route* to restricted water bodies such as lagoons (Braddy, 2001). In terms of mating, the reproductive palaeobiology of eurypterids is now interpreted as more scorpion-like. Braddy and Dunlop (1997; but see Kamenz et al., 2009, for an alternative interpretation) proposed a model whereby the female retrieved a spermatophore from the substrate with her genital appendage for storage in internal spermathecae, and delayed spawning until environmental conditions were optimal to ensure survival of the larva. Braddy and Dunlop also suggested that eurypterids may have been able to mate before their final moult stage, based on the presence of a fully-developed genital appendage in younger males, although they probably would have had less mating success as they were smaller, with less-developed claspers. Conversely, the organ may be developing, but not yet functional, in submature males. Trace fossils provide further support for the mass-moult-mate hypothesis: eurypterid track ways (*Palmichnium*) are generally rare in the fossil record, but sometimes occur in great abundance in the Silurian and Early Devonian (Braddy, 2001). The Muth Formation (Early Devonian) of northern India (Draganits et al., 2001), for example, contains multiple sub-parallel eurypterid track ways, apparently produced during a short time span, indicating *en masse* movement of eurypterids in a similar direction.

The North American xiphosuran *Limulus polyphemus* Linnaeus, 1758 has traditionally been used as a modern analogue for eurypterids – the so-called “*Limulus* paradigm” (Plotnick, 1983 unpublished). (Three other Indo-pacific species with very similar lifestyles and morphology exist within the genus *Tachypleus* [Shuster, 1982], but *Limulus* remains the more studied and more geographically relevant genus.) Although research now favours a eurypterid-scorpion clade, xiphosurans remain the only extant, primarily aquatic chelicerates, and so may provide important clues to eurypterid mating behaviour. Extant xiphosurans mate annually *en masse* at specific breeding sites that coincide with lunar and tidal rhythms (Rudloe, 1980), laying their eggs in clusters of nests along the beach (Shuster, 1982). After hatching, *Limulus* larvae tend to remain in shallow intertidal areas near the beaches where spawning occurred (Shuster, 1982), but as they grow they move away from these nursery areas into deeper waters where they mature into adults. Adults may migrate as far as the continental shelf, to depths of several hundred metres, before returning to the beaches each breeding season. Depending on the species, males will either come ashore already attached to a female or they will arrive separately at the breeding site, only joining once on the beach (Sekiguchi, 1988). Males who fail to find a partner immediately cluster around already attached mating couples in an effort to fertilise the eggs themselves, and where there is an abundance of unattached males the gender ratio may be as high as 14:1 (Rudloe, 1980). As males must compete amongst themselves to fertilise the female’s eggs, their mating success is less than that of the females, who are virtually guaranteed to find a mate. Males will therefore often return to a breeding site repeatedly, whereas females may only visit the breeding site once or twice, completing their breeding activity within a week (Brockmann and Penn, 1992).

The adult male:female ratio outside of breeding sites is about 2:1 compared to roughly 1:1 at juvenile stages (Carmichael et al., 2003); either males moult less, decreasing their potential of mortality during ecdysis (Tester and Carey, 1986; Carmichael et al., 2003), or females remain offshore longer than males, and so are less likely to be sampled unless they are actively spawning (Rudloe, 1980). Although male biased gender ratios have also been noted in spider crabs (Tester and Carey, 1986), this is opposite to the female-dominated populations of several scorpion species (Williams, 1987) where the gender ratio may be as high as 1:3 (Smith, 1966). However, the latter is primarily due to males being subjected to increased predation as they search for a mate away from their home site (Williams, 1987).

Previous discussion of eurypterid salinity tolerance, relevant here due to the hypersaline nature of the Bertie Group, has focused on whether particular groups of eurypterids were euryhaline. Most Stylonurina lived in marginal marine or non-marine environments, whereas the Eurypterina had a much broader environmental distribution; from the mid-Ordovician to the Early Devonian they lived in a range of environments, but then became entirely non-marine (Plotnick, 1999). Some eurypterid genera were probably euryhaline, based on their presence in both hyper- and hypo-saline deposits (Clarke and Ruedemann, 1912; Størmer, 1934, 1976). Although Plotnick (1999, p. 112), questioned this hypothesis, stating, “...no single species is known from localities of different inferred salinities”, Braddy (2001) considered the lack of single species being found in different salinities to be an artefact of taxonomic over-splitting rather than any palaeoecological reality.

### 2.2. *Eurypterus remipes* and *Eurypterus lacustris*

*E. remipes* is found exclusively in the Fiddlers Green Formation of the Bertie Group, whereas *E. lacustris* occurs only in the overlying Williamsville Formation. Their original designation as separate species by Clarke and Ruedemann (1912) has since been subject to debate and various authors have considered them either a single species or sub-species (Kjellesvig-Waering, 1958; Plotnick, 1983 unpublished; Cuggy, 1994; Tetlie and Cuggy, 2007) or separate species (Tollerton, 1992 unpublished; Tetlie, 2006; Tetlie et al., 2007). Tetlie et al. (2007) provided the first evidence for distinct morphological traits, based on eye, carapace and telson shape that could be used to distinguish between *E. remipes* and *E. lacustris*, and supported their retention as separate species. Based on these characters, Tetlie et al. (and Tetlie and Cuggy [2007]) to some degree considered *E. remipes* and *E. lacustris* to be chronospecies rather than distinct sister taxa, following Tollerton (1992 unpublished). The isolation of *E. remipes* and *E. lacustris* in older and younger formations respectively, and apparent morphological distinctions would support this latter theory. Despite a lack of definite consensus on the relationship of these two species, they are considered here to be separate chronospecies derived from a single evolving lineage.

### 2.3. Moults or mortalities?

All arthropods undergo ecdysis during their lifetime in order to grow, some *en masse*, such as trilobites (Speyer and Brett, 1985; Karim and Westrop, 2002) and xiphosurans (Rudloe, 1980), an ancestral group to eurypterids. Eurypterids probably moulted in a manner similar to modern xiphosurans: the marginal suture of the prosoma split apart and the animal emerged anteriorly through the dorsal and ventral exoskeleton (Størmer, 1934; Tetlie et al., 2008). Although both organisms are capable of leaving their exuviae completely intact following ecdysis, eurypterid exuviae are thinner and generally less robust than those of xiphosuran and thus the former are more prone to splitting and disarticulation during the moulting process (see Tetlie et al., 2008, Section 5.1, for a detailed description).

Clarke and Ruedemann (1912, p. 25) interpreted the majority of specimens from New York and Ontario as being “cast exuviae from the frequent moulting of growing individuals”, a view supported by most subsequent authors (i.e. Størmer, 1934, 1976; Kjellesvig-Waering, 1958; Tollerton, 1997; Batt, 1999; Braddy, 2001; Tetlie et al., 2008). Andrews et al. (1974) suggested the single opposing view that the Bertie specimens represent a mass death assemblage following a storm, or similar catastrophic event, though subsequent authors have discounted this (see Braddy, 2001, and Tetlie et al., 2008, for discussion and evidence respectively). Although there are a number of features that may indicate a specimen is a carcass rather than a moult (Tetlie et al., 2008, Table 2), and some specimens from the Bertie Group have been interpreted as being carcasses (see Braddy, 2001, for discussion), they are rare, and the bulk of specimens from the Bertie Group and all of those examined in this study are considered to be shed exuviae.

As most specimens from the Bertie Group are moults rather than carcasses, the relative absence of dead organisms is actually somewhat surprising considering that the chance of mortality is increased during ecdysis (Brandt, 2002). There are various examples of trilobites that died or became disfigured whilst moulting (Brandt, 2002), and mortality has also been shown to occur most often during ecdysis in at least two species of extant scorpion (De Vojoli, 1991; Bullington, 1996), and in studies on both *Limulus* (Carmichael et al., 2003), and spider crabs (Tester and Carey, 1986). Possible explanation for lack of carcasses in the Bertie Group is discussed below.

#### 2.4. Geology and palaeoecology of the Bertie Group

The Bertie Group is exposed from eastern New York to the Niagara Peninsula of Ontario and consists primarily of massive dolostones, within which are occasional waterlime beds (Cieurca, 1973, 1978; Hamell, 1982). Cieurca (personal communication) describes these waterlime beds as “very fine-grained argillaceous dolostone[s] with some fine quartz... [usually] formed in hypersaline conditions”. Two formations are of particular relevance to this study: the Fiddlers Green Formation (also known as the Falkirk Member in Ontario), and the Williamsville Formation (see Tetlie et al., 2007, for a map and stratigraphic column of the Bertie Group, and the position of eurypterid-containing beds). The Fiddlers Green Formation is divided into several members, of which only the Phelps Member yields abundant eurypterid fossils (Cieurca, 1978); that member can be traced from Phelps to its easternmost exposure at Passage Gulf, in New York State. Centrally and westward towards Buffalo and Ontario, the Phelps Member is absent, primarily due to erosion, but in Ontario, eurypterids are still found within other layers of the Fiddlers Green Formation. The Williamsville Formation, another waterlime, varies in its facies characteristics across New York State (Cieurca, 1978). In the eastern and central regions, *E. lacustris* is generally absent, but towards the west, in the Buffalo and Ontario-Williamsville regions, they are abundant. Where present, eurypterids are only found in the uppermost beds – specifically within the A Member – nearing the boundary with the overlying Cobleskill-Akron Formation.

The depositional setting of the Bertie Group has been subject to various interpretations (see Andrews et al., 1974; Braddy, 2001, for reviews), though the Phelps Member and Williamsville Formation are generally considered to be predominantly brackish to marine intertidal settings that occasionally became hypersaline. Andrews et al. (1974) considered the Fiddlers Green Formation to represent a range of habitats, from shallow water subtidal lagoonal to supertidal flats, as denoted by the presence of eurypterids and mud cracks respectively; Hamell (1982) suggested salinity might have been lower within the Williamsville Formation compared to the Phelps Member due to an absence of salt hoppers.

In both units, eurypterids tend to be found within conchoids (Fig. 1), where the waterlime has weathered into conchoidally-fractured layers

(Cieurca, 1978). Some indication of tidal activity can be inferred from specimens where whole animals or disarticulated sections, such as telsons, have become aligned within these conchoids (Cieurca, 1978; Tollerton, 1997). Batt (1999, p. 62) noted that these conchoids “may have been shallow depressions orientated parallel to shore in which cast-off moults and the remains of other organisms were accumulated during tidal processes”.

Within the Bertie Group, the most abundant arthropods are *Eurypterus* spp. (including *E. dekeyi*); in addition, other eurypterids (*Pterygotus* and *Dolichopterus*), three xiphosuran species, and at least one species of marine scorpion have also been found (Clarke and Ruedemann, 1912; Tollerton, 1997; Dunlop et al., 2008). Some plants have also been found including *Cooksonia* and various algae such as *Medusaegraptus* (Cieurca, 1978; Tollerton, 1997). For example, at least one slab collected from the Williamsville Formation (BMS-E1657) contains a specimen of a eurypterid entangled in an algal mass.

#### 2.5. Taphonomic implications

Biostratinomic processes resulting in taphonomic bias such as transport, reorientation, disarticulation and fragmentation of specimens (Brett and Baird, 1986; Speyer and Brett, 1988), are important considerations when interpreting the Bertie eurypterid assemblage in the context of the mass-mate-moult hypothesis. This is especially true when considering lightweight moults that are more likely to be subjected to hydrodynamic sorting, transport and fragmentation than heavier carcasses (Mikulic, 1990; but see McCoy and Brandt, 2009). Transport and disarticulation of moults may obscure or alter any distribution of remains that “might otherwise be considered behaviourally controlled” (Mikulic, 1990, p. 20), such as mass mating and moulting. At the same time, taphonomic processes and disarticulation patterns can be helpful in inferring the depositional environment (Brett and Baird, 1986; Brandt, 1989; Tollerton, 1997). Although Tollerton (1997) previously noted the paucity of detailed taphonomic data from the Bertie eurypterid assemblage, Tetlie et al. (2008) has since carried out an extensive taphonomic census, examining the disarticulation pathway of several thousand specimens, and this is also investigated further herein, albeit on a smaller scale.

As the Bertie Group eurypterid specimens are generally interpreted as a moulted assemblage, this raises the questions of where the moulting took place in relation to burial of exuviae. Caster and Kjellesvig-Waering (1964) suggested that generally, eurypterids would have required a quiet and current-free area to moult. Within

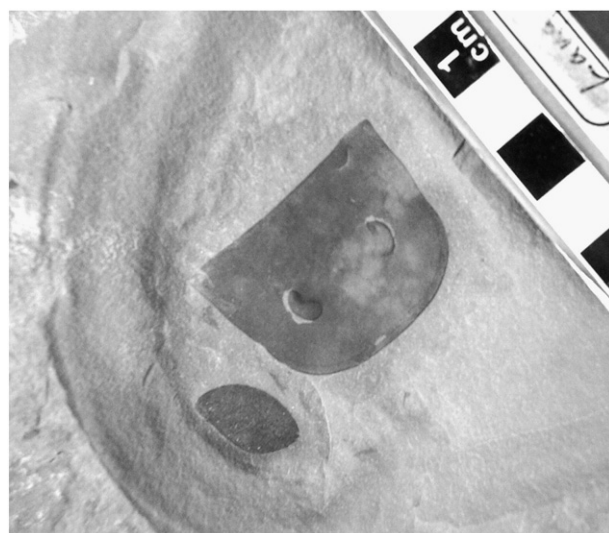


Fig. 1. Isolated prosoma of *Eurypterus remipes* from Lang's Quarry, Litchfield, New York (Phelps Member, Fiddlers Green Formation) in conchoidal depression. Scale bars in cm.

New York State and surrounding areas, Andrews et al. (1974) suggested that the eurypterids lived in a subtidal habitat, whereas Hamell (1982) suggested that eurypterids found in the Phelps Waterlime Member and Williamsville Formation most likely lived in the intertidal zone, some distance south of their final resting place. The general lack of regular ripple marks and presence of evaporites within some layers of the Bertie Group indicate that the depositional setting in which exuviae were buried may have been quite shallow and calm, and conforms to that specified by Caster and Kjellesvig-Waering (1964). However, the abundant accumulations of primarily disarticulated eurypterid exuviae in the Bertie Group – only 5% of a sample of 1771 *Eurypterus* sp. exuvial elements from Passage Gulf, NY examined by Tetlie et al. (2008) were complete specimens – and their occurrence in tidal windrows (as termed by Ciuca, 1973) point towards transport following ecdysis, rather than immediate burial. Transport would also distance moults from any mortalities that presumably occurred in the same location.

If exuviae were transported, it is difficult to discern how far they travelled based on the relative frequency of both articulated and disarticulated specimens, often on the same bedding plane. Allison (1986) and Tollerton (1997, p. 257) warned against using the degree of disarticulation of a specimen as “an indicator of distance of transport or duration of agitation”, however experiments on Recent arthropod moults and carcasses may offer some clues as to the durability of arthropod exuviae and degree of transport before burial in the Bertie Group. Mikulic (1990) showed that a relatively slow current is capable of transporting moults, with even brief transport causing disarticulation to some extent. This is in contrast to experiments on marine arthropod mortalities by Allison (1986) and Plotnick (1986, 1999), Plotnick et al. (1988) and Babcock and Chang (1997, p. 23), that show that carcasses may disarticulate relatively slowly, over “days to weeks to months, rather than in hours or days” in aquatic settings. More recently, McCoy and Brandt (2009) showed that during continuous wet tumbling in smooth canisters, scorpion exuviae (possibly the best proxy for eurypterid exuviae) exhibited some degree of disarticulation in six days, and became completely disarticulated within 12 days (and partly to completely disarticulated in less time when using invaginated tumblers). The same experiment also showed carcasses and moults disarticulated in roughly the same time under the same conditions.

Vertical orientation of specimens (i.e. ventral or dorsal-up) may also help to determine current speed, and therefore the degree of transport before burial (Brett and Baird, 1986). In the case of eurypterids, it may also indicate a preferred orientation during ecdysis. Unfortunately, the regular splitting of eurypterid fossils into part and counterpart, and the fact that their way-up orientation is almost never recorded, hampers determination of final orientation from museum specimens. Nevertheless, some authors have recorded orientation: Batt (1999), in his study of 33 *E. remipes* moults, found that nearly 70% were recovered ventral-up; Tollerton (1997) also noted a similar proportion in a smaller sample. Tetlie et al. (2008), in a much larger sample (N=152), noted a slightly more predominant dorsal-up orientation amongst more complete specimens from the Ridgemount Quarry, Ontario (Williamsville Formation), but they found no statistically significant difference overall. Tollerton (1997), and later (Tetlie et al., 2008), suggested two potential causes for this pattern: either *Eurypterus* preferentially carried out ecdysis whilst supine, resulting in a predominance of ventral-up specimens, or *Eurypterus* behaved in a *Limulus*-like manner, shedding its exuviae in a prone position, whereupon exuvial orientation was occasionally reversed during current-driven transport.

Tetlie et al. (2008) postulated that the fragmentary cuticle remains that are found alongside more articulated specimens may have been either the result of time-averaging and physical disturbance, or perhaps predation or even cannibalism as seen in some other arthropods and eurypterids (e.g. Caster and Kjellesvig-Waering, 1964). Although there is no direct evidence of the last in the Bertie

Group, it is worth noting that McCoy and Brandt (2009, p. 315) showed that under dry conditions, tumbling of scorpion exuviae in canisters resulted in “reduced to ragged-edged, broken exoskeletal pieces rather than separated, unbroken tergites” in two to three days. It is assumed here that most eurypterid exuviae from the Bertie eurypterid assemblage remained submerged from ecdysis to burial, but given that both the Phelps Waterlime Member and Williamsville Formation have been interpreted as being intertidal settings, exuvial desiccation due to exposure to air and movement by wind may have been an additional source of transport and fragmentation.

The extent that preservational bias influenced the abundance of specimens found in the Bertie Group has also been questioned. Brooks (1957) argued that chitinous (non-mineralized) exoskeletons are rarely preserved in typical marine sediments, and whilst the Bertie Group does not necessarily represent a typical marine environment, the abundance of eurypterid exuviae here is still exceptional. This abundance may be explained in several ways. Plotnick (1986) noted that a lack of predation and bioturbation reduces the chances of an organism being exhumed after burial. Although some beds within the Bertie Group do contain extensive burrowing, eurypterid remains are not found within them (Andrews et al., 1974). Predators present in the Bertie Group include other eurypterids (pterygotids) and orthocone nautiloids. Remains of the former are often found alongside *Eurypterus* moults; however, nautiloids represent a very small percentage of the fauna, and may not have been able to tolerate the higher salinity levels of the Bertie, similar to modern cephalopods (Tetlie et al., 2008). Babcock et al. (2003) considered the absence of bioturbation, and the lack of effective microbial decomposition as an explanation for the excellent preservation of xiphosurid exoskeletons from some sites. Dunlop et al. (2008) also came to the latter conclusion, citing the elevated hypersalinity and subsequent lack of chitinophosphatic bacteria in the Bertie Group as possible explanation for the excellent preservation of chitinous eurypterid and scorpion cuticle there. As bacterial deterioration of connective tissues is an important cause of disarticulation (Speyer and Brett, 1988; but see Gupta et al., 2009 for an exception), its absence from the beds containing eurypterids may have allowed burial of articulated specimens before they could be broken down. Recent experiments by Mutel et al. (2008) and Parsons-Hubbard et al. (2008) support the premise that hypersaline environments can create sites of excellent preservation. If shed exuviae were transported into these environments following ecdysis, chances of preservation may have been greatly increased. Conversely, the composition of the cuticle itself may have played a role. Gupta et al. (2007) determined that eurypterid cuticle was compositionally similar to that of extant horseshoe crabs and scorpions, and showed that microbial breakdown in eurypterid cuticle post-burial may have been limited by *in situ* polymerization of lipids, and the subsequent creation of non-hydrolysable macromolecules, which are lacking in living organisms.

In summary, the excellent preservation of specimens in the Bertie Group may be attributable to several factors including rarity of bioturbation, the fact that most specimens were moults and not likely to be subjected to predation, a slow disarticulation rate due to absence of effective microbial decomposition, possible transport into hypersaline lagoon-like settings from lower salinity estuary-like environments, and biochemically-strengthened cuticle following burial. Furthermore, the above conditions point towards mechanical (rather than biological or chemical) breakdown of cuticle as the primary source of disarticulation and fragmentation of eurypterid specimens in the Bertie Group. If eurypterid exuviae was structurally similar to that of scorpions as Gupta et al. (2007) indicate, this, along with the varying vertical orientation of specimens and lack of sorting (as indicator of long-distance or strong tidal transport) seen in previous studies of *E. remipes* (e.g. Andrews et al., 1974), indicates that a slow, low energy current most likely kept the exuvia moving along the substrate rather than in the water column, and that the distance of transport before burial probably was not great. The

results of McCoy and Brandt (2009) suggest that (like that of scorpions) eurypterid exuviae may have been durable enough to withstand transport in the water column away from the site of ecdysis for perhaps up to a week prior to burial whilst remaining intact. Given the above environmental conditions, it seems plausible that any mechanical breakdown of cuticle resulting in disarticulation and fragmentation occurred within this timeframe.

### 3. Materials and methods

#### 3.1. Localities and repositories

Specimens used in this study came from three localities, each exposing different parts of the Bertie Group (see Cuggy, 1994, Fig. 2 for quarry locations): (1) Lang's Quarry, Litchfield, New York State (Fiddlers Green Formation, Phelps Member), held in the Royal Ontario Museum (ROM), Toronto; (2) Bennett Quarry, Buffalo, New York State (Williamsville Formation), held in the Buffalo Museum of Science (BMS), Buffalo, New York State; and (3) Cambell Quarry and Ridgemoor Quarry and vicinity, Fort Erie District, Bertie Township (herein referred to as "Ft. Erie District"), Ontario (Fiddlers Green and Williamsville Formations), also held in the ROM. Total combined sample size from all three locations for size-frequency measurements and gender assignment was 632, and an additional 23 *Eurypterus* sp. from the above three localities were included in the disarticulation analysis.

#### 3.2. Data analysis

All specimens were measured using ImageProPlus (ver. 4.1, 1999). Data were collated using OpenOffice.org 2.4 (ver. 2.4.1, 2008) and analysis was carried out using both OpenOffice.org and PAST (ver. 1.26, 2004). Repeat measurements of prosoma gave an error interval of  $\pm 0.5$  mm ( $N = 100$ ).

During this study, at least one of the four body tagmata (i.e. prosoma, preabdomen, postabdomen or telson) had to be complete for the specimen to be measured. Five measurements were taken on a complete dorsal-up individual (Fig. 2). Prosoma length and total body length (minus telson) were taken only from specimens showing no

deformation or distortion, i.e. where each tergite was fully visible and not obviously crumpled or compressed. Preliminary measurements here (and elsewhere, see Andrews et al., 1974 for discussion) show that prosoma length and total body length (minus telson) share a linear relationship, so assuming the prosoma was present, the total body length (minus telson) from a partially disarticulated, distorted or telescoped (i.e. unnaturally compressed) specimen could be extrapolated using the length of the prosoma against complete specimens. This method was not used to extrapolate prosoma lengths from ventral-up specimens, however, resulting in differing sample sizes for body lengths versus prosoma lengths. Ventral-up specimens accounted for ~15% (96:632) of the total sample size, and of these, gender was noted on 77% (74:96). Both articulated and isolated *Eurypterus* telsons from Lang's Quarry and Bennett Quarry were included and measured. No telsons were present in the Ft. Erie District material. The degree of articulation for all specimens at a given location was also recorded, based on articulation of the body units, and presence/absence of telson and appendages.

Arthropod fossils are typically assigned to specific instar groups based on either distinct instar-specific morphologies or discrete clusters in morphological measurements. However, even in a normally distributed arthropod population, there will be a range of sizes around each instar class that increases as organisms grow larger (Hunt and Chapman, 2001). Clarke and Ruedemann (1912) simply assigned eurypterid specimens qualitative ages (e.g. "juvenile", "adult"). Andrews et al. (1974) noted the difficulty in attempting to determine eurypterid instar stages due to overlap, although they ultimately produced nine discrete instar stages for *E. remipes*. Tollerton (1992 unpublished) designated only three growth stages based on prosoma length for simplicity. The data in this study were continuous, with no apparent clusters or known instar stages from which to calculate the rest (using Dyar's curve [Hutchinson and Tongring, 1984], for example), hence assignment of specific instar class size ranges was not attempted. Instead, specimens were conservatively classified as larval (0–14 mm), juvenile (15–30 mm) or adult (>30 mm) based on prosoma length. These size classes equate approximately to a body size (minus telson) of <60 mm, 60–120 mm and >120 mm, and instar stages I–III, IV–VII, and VII–IX (cf. Andrews et al., 1974), respectively.

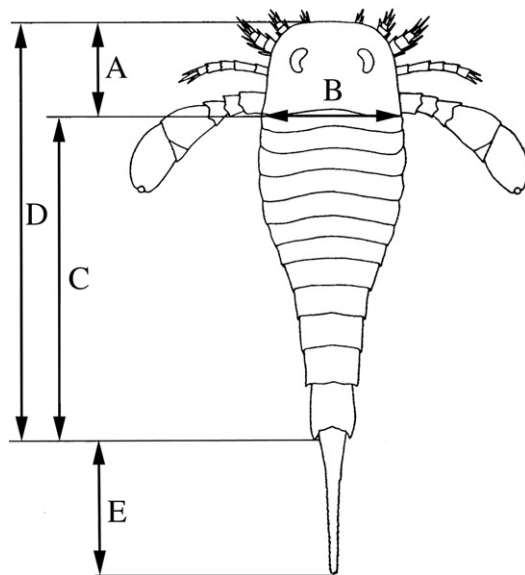


Fig. 2. Diagrammatic representation of *Eurypterus remipes* and measurements taken in this study; A, prosomal length; B, prosomal width; C, opithosomal length; D, total body length (excluding telson); E, telson length. Modified from Andrews et al. (1974).

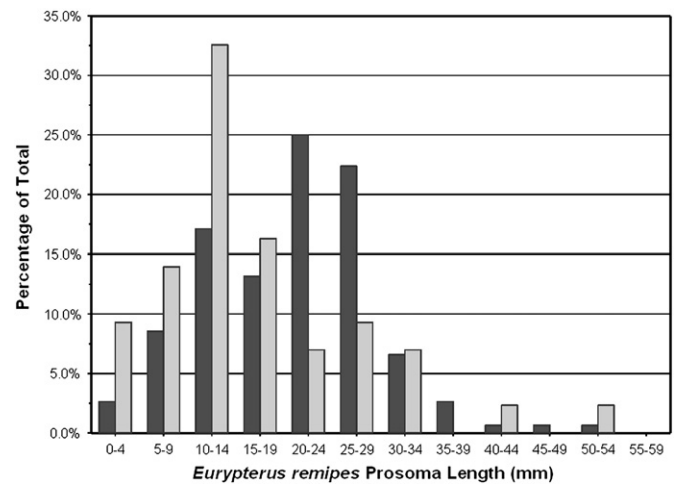


Fig. 3. Normalised size-frequency distribution of prosomal length in *Eurypterus remipes* from Lang's Quarry (Phelps Member, Fiddlers Green Formation), New York ( $n = 152$ ; ROM collection) indicated by dark grey, and Ft. Erie District (Falkirk Member, Fiddlers Green Formation), Ontario ( $n = 43$ ; ROM collection) indicated by light grey.

4. Results and interpretation

4.1. Size and gender distribution

Sample sizes for all measurements are roughly similar with the exception of those from the Ft. Erie District. The overall distributions for the prosoma length of *E. remipes* (Fig. 3) and *E. lacustris* (Fig. 4) from Lang's Quarry and Bennett Quarry respectively are similar in that the entire range of growth stages from larval to adult are represented in both species from both localities. The *E. remipes* and *E. lacustris* materials from Ft. Erie District show a reduced size range, particularly in the latter sample, which excludes the smallest and largest growth stages, a feature also reported by Batt (1999).

In terms of size–frequency distribution of prosoma length, *E. remipes* shows a noticeable right-skew (cf. Andrews et al., 1974), compared to the roughly normal distribution of *E. lacustris*, and displays a larger proportion of larval and juvenile sizes compared to adult. *E. remipes* from both localities shows an increased number of prosomae in the 10–14 mm length range and also exhibits a slight reduction in the 15–19 mm prosoma size class, the latter considered here to be the boundary between the juvenile and adult size. *E. lacustris* from Bennett Quarry shows no significant change in the number of specimens from the 10–14 to 20–24 mm (i.e. juvenile) size classes, whereas *E. lacustris* from the Ft. Erie District shows a noticeable spike in the 20–24 mm size class (as well as the 30–40 and 40–44 mm size classes). These frequency spikes are most likely the result of the small sample size from that location rather than population reality. Average prosoma length of *E. remipes* was 21 mm (n = 152) from Lang's Quarry, and 17 mm (n = 43) from Ft. Erie District. The average prosoma length of *E. lacustris* was 31 mm (n = 221) from Bennett Quarry, and 28 mm (n = 12) from Ft. Erie District.

Size–frequency distributions of body length (minus telson) for *E. remipes* (Fig. 5) and *E. lacustris* (Fig. 6) generally repeat the pattern seen in prosomal size–frequency distribution, albeit at a larger scale and with a slightly larger total sample size. *E. remipes* again shows a right-skew and a sudden drop in larger adult body lengths compared to *E. lacustris*, which shows a roughly normal distribution. Given the smaller sample size of *E. remipes* from Ft. Erie District compared to that of Lang's Quarry, it is notable that the highest distribution peak from the former is within the 60–69 mm range, the same range in which the frequency of body length of *E. remipes* from Lang's Quarry dips. The *E. lacustris* material from the Ft. Erie District again shows sharp peaks in several size classes, again thought to be the result of a small sample size. Average body length of *E. remipes* was 87 mm (n = 188) from Lang's Quarry, and 74 mm (n = 43) from Ft. Erie

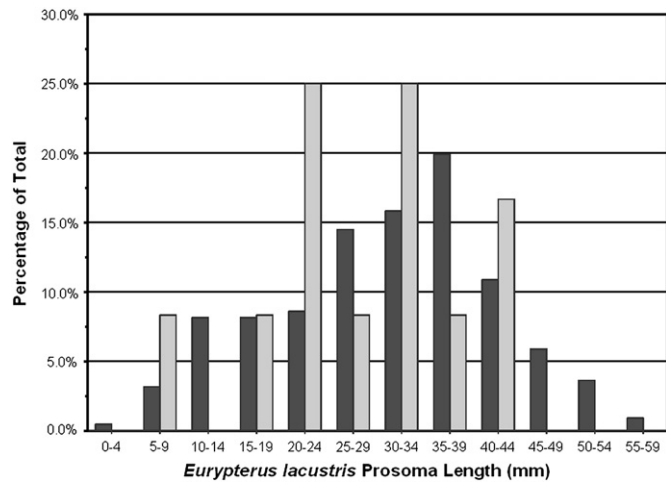


Fig. 4. Normalised size–frequency distribution of prosomal length in *Eurypterus lacustris* from Bennett Quarry (Williamsville Formation), New York (n = 221; BMS collection), indicated by dark grey, and Ft. Erie District (Williamsville Formation), Ontario (n = 12; ROM collection), indicated by light grey.

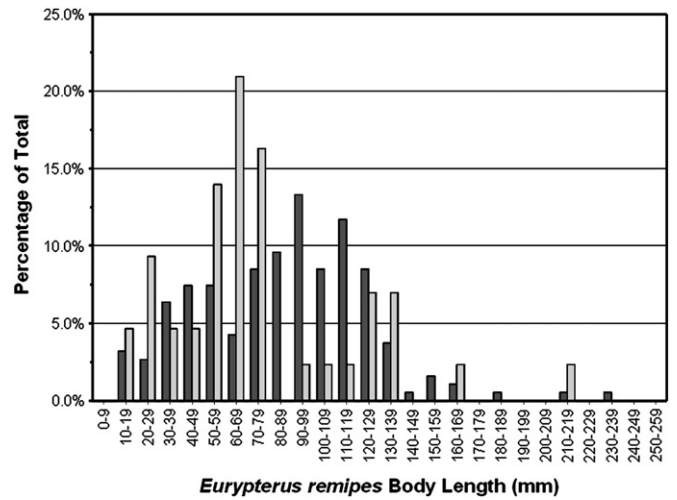


Fig. 5. Normalised size–frequency distribution of body length (minus telson) in *Eurypterus remipes* from Lang's Quarry (Phelps Member, Fiddlers Green Formation), New York (n = 188; ROM collection), indicated by dark grey, and Ft. Erie District (Falkirk Member, Fiddlers Green Formation), Ontario (n = 43; ROM collection), indicated by light grey.

District. Average body length for *E. lacustris* (based only on length extrapolated from prosoma) was 136 mm (n = 212) from Bennett Quarry, and 114 mm (n = 43) from Ft. Erie District.

The pattern of the size–frequency distribution of isolated and attached telsons from *E. remipes* from Lang's Quarry (N = 79; average = 25 mm) and *E. lacustris* from Bennett Quarry (N = 75; average = 42 mm) (Fig. 7) is generally similar to that of the prosoma and body lengths. Telsons from Bennett Quarry show a particularly prominent left-skewed size–frequency distribution, and although there is a disproportionate frequency peak in the Lang's Quarry material between 20 and 24 mm, they otherwise show a roughly normal distribution.

It was possible to determine genital appendage type in ~12% of the total *Eurypterus* sample (N = 632), and following Braddy and Dunlop's (1997) assignment of the type A appendage as female, and Type B as male, a significant predominance of females was seen at all localities (Chi-squared test; df = 1, p < 0.01) (Table 1). Kjellesvig-Waering (1958) and Tetlie et al. (2008) also noted that, where identifiable, most specimens of *E. remipes* showed the type A (i.e. female) genital

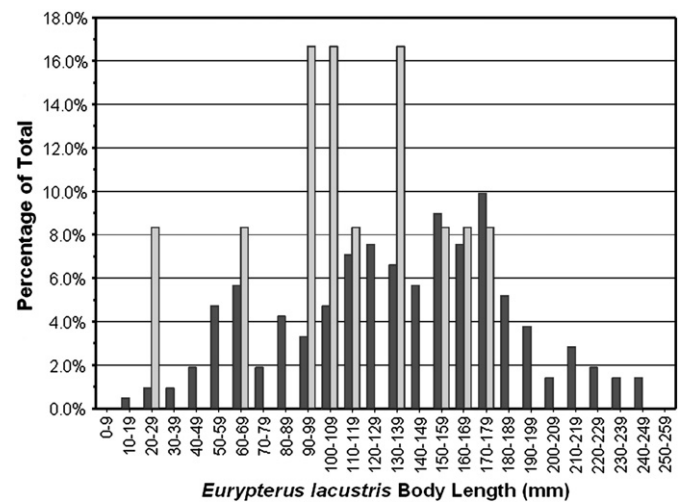
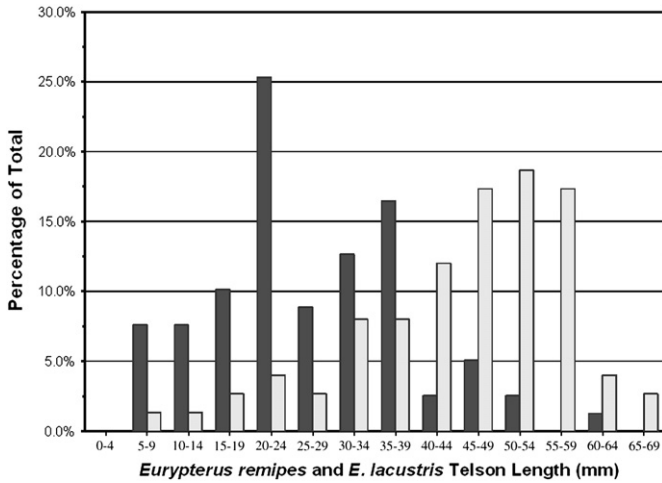


Fig. 6. Normalised size–frequency distribution of body length (minus telson) in *Eurypterus lacustris* from Bennett Quarry (Williamsville Formation), New York (n = 212; BMS collection) indicated by dark grey, and Ft. Erie District (Williamsville Formation), Ontario (n = 12; ROM collection), indicated by light grey.



**Fig. 7.** Normalised size-frequency distribution of isolated telson lengths in *Eurypterus remipes* from Lang's Quarry (Fiddlers Green Formation, Phelps Member), New York (n = 79; ROM collection) indicated by dark grey, and *E. lacustris* from Bennett Quarry (Williamsville Formation), N.Y. (n = 75; BMS collection), indicated by light grey.

appendage. Female specimens also tended to be larger, although this may be an artefact of the difficulty in determining the gender of the smallest specimens.

**4.2. Patterns of disarticulation**

Although whole or nearly complete specimens with a prosoma were preferentially chosen for this study, enough specimens with varying degrees of disarticulation were examined for a general pattern of disarticulation to be developed in a manner similar to that of Tetlie et al. (2008). The prosoma was the most commonly preserved isolated tagma (507:655) in the samples from all three localities (Table 2). A carapace with only the first tergite attached was a common association from all three locations (54:655), and despite having the smallest sample size, the *Eurypterus* prosomae from Ft. Erie District had the highest occurrence of this type of disarticulation (11:69). Batt (1999) and Tetlie et al. (2008) both noted this pattern of disarticulation in *Eurypterus* from the Bertie Group, and the later suggested that the frequency of this association, and non-random nature of the split with the opisthosoma at segment 2, was probably the direct result of ecdysis rather than environmental disturbance. Kues and Kietzke (1981, Table 1) found a similar pattern in a different eurypterid assemblage and observed that the number of specimens preserved with "Prosoma + Preabdomen" attached was second only to those with isolated prosomae. Splitting of the ventral plates, something frequently observed but not quantified in this study, is also thought by Tetlie et al. (2008) to be a result of ecdysis. Following the prosoma, the preabdomen was preserved less often, and the postabdomen least often in this study. The presence of prosomal appendages was variable and not necessarily linked with the presence

**Table 1**  
Distribution of *Eurypterus* type A and type B appendages from Lang's Quarry (LQ), Litchfield, New York, Phelps Member, Fiddlers Green Formation; Bennett Quarry (BQ), Buffalo, New York, Williamsville Formation; Campbell Quarry and Ridgemount Quarry, Ft. Erie District (FED), Ontario, Fiddlers Green and Williamsville Formations.

Location	Species	(n)	Type B (% of n)	Type A (% of n)
BQ	<i>E. lacustris</i>	41	24 (59%)	17 (42%)
LQ	<i>E. remipes</i>	28	22 (79%)	6 (21%)
FED	<i>E. lacustris</i>	1	1 (100%)	0
	<i>E. remipes</i>	4	4 (100%)	0
	Total	74	51 (68%)	23 (32%)

**Table 2**  
Proportion of disarticulation amongst *Eurypterus* specimens (N = 655) used in this study; P, prosoma present; + 1, with first tergite attached; Ps, prosoma (carapace) only; Pr, entire preabdomen; Ppr, partial preabdomen; Po, entire post-abdomen; Ppo, partial post-abdomen; T, telson; Sw, swimming appendages; Oa, other appendages. N.B. P, P + 1 and Ps are mutually exclusive.

Location	P	P + 1	Ps	P + Pr	P + Ppr	P + Po	P + Ppo	P + T	P + Sw	P + Oa
Bennett Quarry, NY (n = 306)	224	28	38	205	24	159	34	110	135	59
% of total	44%	52%	64%	45%	35%	42%	55%	45%	37%	28%
Lang Quarry, NY (n = 280)	237	15	12	207	44	177	24	116	187	137
% of total	47%	28%	20%	45%	64%	47%	39%	47%	52%	64%
Fort Erie District, ON (n = 69)	46	11	9	46	1	42	4	20	39	18
% of total	9%	20%	15%	10%	1%	11%	6%	8%	11%	8%
Total (N)	507	54	59	458	69	378	62	246	361	214
Percent of N	77%	8%	9%	70%	11%	58%	9%	38%	55%	33%

of other tagma, although generally appendages were lost before the body tagma disarticulated.

Although the above results indicate no storm or current driven (i.e. mechanical) sorting, the sharp peak in the size-frequency distribution of telsons from Lang's Quarry may indicate some taphonomic bias. Isolated, as well as articulated telsons were included in this study, and so this frequency peak may be due to current driven size-sorting of isolated telsons. The alignment of isolated telsons in windrows, as noted by Cuirca (1978) and Batt (1999), also supports this.

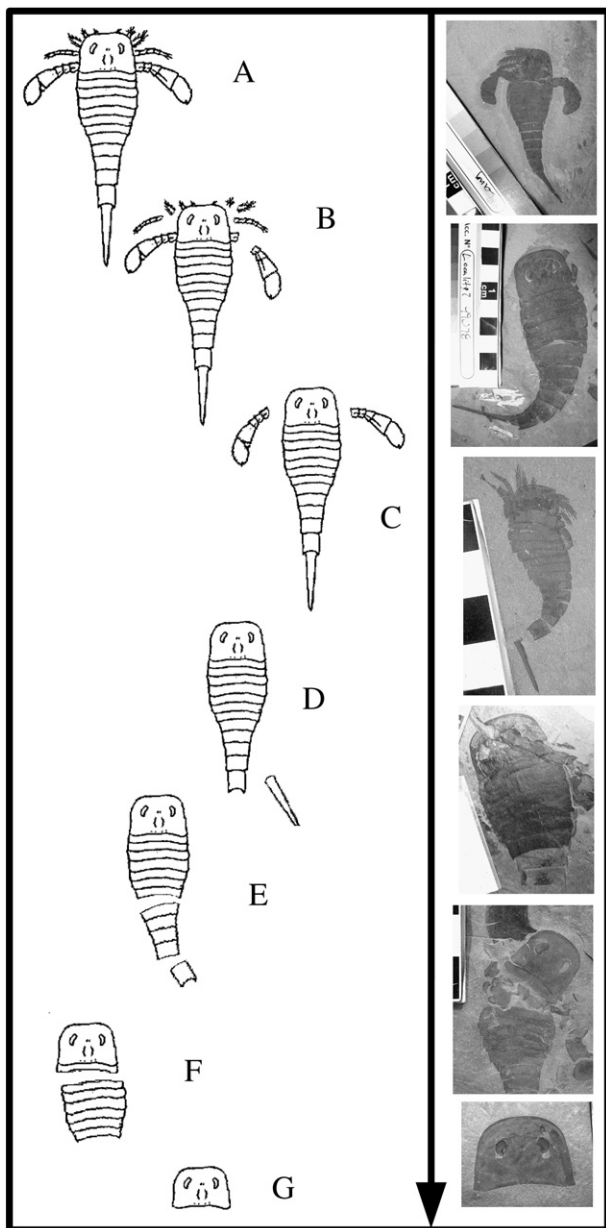
Another observation of this study was the higher proportion of telescoped *Eurypterus* specimens from Bennett Quarry compared to the other localities. Distinguishing telescoping was sometimes difficult due to the range of preservational quality, but at least 10% (n = 306) of the specimens from Bennett Quarry were unequivocally telescoped. Interestingly, the post-abdomen was not usually compressed in the same specimen. Within the entire sample, there were at least two specimens where the post-abdomen was compressed underneath the preabdomen, at 90° or more (Fig. 8). In one example, the abdomen is bent in such a way that the anterior and posterior parts of the animal were parallel; the telson adjacent to the anterior end. Størmer (1976) also noticed this in several different species from the Alken assemblage in Germany, and considered this evidence for transported moults as he did not believe that mortalities could flex to such an extreme degree. Only one specimen from the entire sample was determined to be a mortality, considered further evidence that specimens from the Bertie Group are predominantly moults rather than mortalities.

Based on the results of this study, a pattern of exuvial disarticulation is herein proposed with six distinct stages (Fig. 9). A broadly similar pattern



**Fig. 8.** *Eurypterus remipes*, bent over 180°, from Lang's Quarry, Litchfield, New York (Phelps Member, Fiddlers Green Formation). Scale bars in cm.

of disarticulation has been seen in other non-mineralized arthropods such as *Naraoia* (Babcock and Chang, 1997) and *Limulus* (Babcock and Chang, 1997; Babcock et al., 2003). In *Limulus*, mortalities take up to 64 days before complete disarticulation occurs (Babcock et al., 2003), but can also behave hydrodynamically similar to a moult after only 7 days. Hence, whilst no time frame can be given for the duration of each stage proposed herein, the time taken for complete disarticulation would have been dependent on the amount of agitation in the environment. Based on the experimental primarily results discussed in Section 2.5, it would seem plausible that, under calm conditions, complete disarticulation could have occurred within seven days, whereas current or storm-driven agitation could have caused disarticulation almost immediately. The model proposed here, combined with similar studies (e.g. Tetlie et al., 2008) may prove useful when analysing other eurypterid assemblages where whole or partially disarticulated specimens are present.



**Fig. 9.** Simplified disarticulation sequence of *Eurypterus* in the Bertie Group of New York and Ontario; A, fully articulated specimen; B, swimming appendages and other appendages begin to disarticulate; C, loss of all appendages; D, telson becomes disarticulated; E, post-abdomen and individual tergites begin to become disarticulated; F, preabdomen becomes disarticulated, typically leaving first tergite attached to prosoma; G, prosoma is last remaining intact tagma. Scale is in cm.

## 5. Discussion

### 5.1. Size-frequency distribution

Our results from the Fiddlers Green and Williamsville pools (*sensu lato* Clarke and Ruedemann, 1912) do not fit into the distribution expected in our *a priori* results for a moulting and breeding ground. Though the material from Lang's Quarry does show a slight dip in the size-frequency distribution at the assumed transition size for juvenile to adult (15–19 mm), there is no distinct bimodal distribution of small larval and larger adults as would be expected in a typical mating and nursery area. The unimodal and roughly normal population distribution seen here, particularly apparent in the *E. lacustris* material from the Williamsville Formation, also does not fit with the size-segregated moult assemblages seen at other eurypterid (e.g. Kues and Kietzke, 1981), or trilobite (Speyer and Brett, 1985; Karim and Westrop, 2002) assemblages. Instead, we see an abundance of moults from juvenile and adult-sized specimens, with more adults present in the material from the Williamsville Formation than in the Fiddlers Green Formation. Størmer (1976) suggested that the absence of the very smallest larval stages in the study by Andrews et al. (1974) was due to deposition of eggs (and subsequent larval growth) in a shallow, arenaceous environment, thus limiting the chances of nests, eggs and the smallest instars ever being preserved. Whilst it is clear that the smallest larval stages will always be rare, larval forms are present in this study, and at sizes smaller than those previously noted by Andrews et al. (1974). Therefore, when considering both the presence of the very smallest larval instars, and the overall range of exuviae sizes found together, we still see support for the hypothesis of the Phelps Member and Williamsville Formations as depositional settings very close to a eurypterid breeding ground, arenaceous or otherwise. The normal, rather than expected bimodal population, and relative abundance of juvenile-adult sizes may be explained by time-averaging and a subsequent blurring of the divisions between instars, or transport before burial (see Section 5.3).

The geographic position of the localities, and the depositional environment of their respective formations may also account for the size-frequency distribution of juvenile-adult stages seen here: the right skew of the size-frequency distribution of the *E. remipes* specimens from the Fiddlers Green Formation may indicate a shallower environment, closer to the larval nursery, whilst the more normal distribution of the specimens from the Williamsville Formation may indicate that it was further away from the breeding grounds and nearer to the deeper habitat of adult *E. lacustris* specimens.

In one sense, these results concur with the original observation made by Clarke and Ruedemann (1912) on the paucity of smaller specimens from the Buffalo pool (i.e. Williamsville Formation), although this idea belies the current theory that *E. remipes* and *E. lacustris* are two different chronospecies separated in location and age, rather than concurrent populations.

### 5.2. Gender ratio

The gender bias seen in our results, though significant, does not immediately fit with our prediction of male dominance, as seen in studies of living *Limulus* (e.g. Rudloe, 1980; Carmichael et al., 2003). Whilst this ratio is similar to that of some adult scorpion populations, female predominance in scorpions may be linked to their more terrestrial lifestyle – something Silurian eurypterids do not share – and increased predation of males (Williams, 1987). It is interesting to speculate whether male eurypterids were also more susceptible to predation by females and other organisms, but this is difficult to test given the general absence of unequivocal mortalities in the Bertie Group. In *Limulus* (Carmichael et al., 2003) and spider crabs (Tester and Carey, 1986), the gender ratio becomes increasingly male-dominated with each successive instar class. For *Limulus*, in particular,



the male-dominated gender ratio at adult stages is either due to males moulting less frequently, thus decreasing their potential of mortality during ecdysis (Carmichael et al., 2003), or females remaining offshore longer than males unless they are actively spawning, and so less likely to be sampled (Rudloe, 1980). In the context of the mass-moult-mate hypothesis (Braddy, 2001), this may point towards females remaining longer in the nursery areas, accounting for prevalence of female exuviae in this study and elsewhere (e.g. Kjellesvig-Waering, 1958; Tetlie et al., 2008).

Of course, in light of our results, this version of the mass-moult-mate hypothesis relies on the currently accepted type A as female and type B as male gender determination, and a scorpion-like mating behaviour that would make limulids an inappropriate analogue (even if they are the most closely related extant marine arthropod). Kamenz et al. (2009), however, have suggested that the accepted type A/type B designations should be reversed; that these reproductive organs actually represent males and female specimens respectively, whilst still supporting a scorpion-like mating pattern. This would create a breeding site with a predominance of males and fewer females and would have implications for the mass-moult-mate hypothesis (see Section 5.4 for discussion).

### 5.3. Environmental influence

According to the mass-moult-mate hypothesis (Braddy, 2001), increased salinity tolerance would be a prerequisite for eurypterids that came to mate in the shallow, marginal and occasionally hypersaline settings of the Bertie Group. Although we cannot test this directly, we can infer it from their extant relatives. Recent xiphosurans are tolerant of wide natural temperature (<0 °C to 40 °C) and salinity ranges (5‰ to fully marine) (Reynolds and Casterlin, 1979), and they also have high tolerance to experimental temperature and hypersalinity, particularly as larvae (Ehlinger and Tankersley, 2004). Growth rate is also affected by temperature and salinity, with slow and rapid growth associated with low and high salinities and temperatures respectively (Jegla and Costlow, 1982). If, like *Limulus*, larval eurypterids were more tolerant of temperature and salinity changes most likely to occur in a shallow hypersaline lagoon, the Bertie Group, with its variable salinity, would have been an ideal nursery setting for larval and juvenile development. As older limulids also have tolerance, albeit decreased, to changes in temperature and salinity (Ehlinger and Tankersley, 2004), adult eurypterids may also have been able to venture into such hypersaline environments, at least temporarily, to mate. Decreased salinity in the younger Williamsville Formation compared to the older Phelps Waterlime Member, and a subsequent increase in resources may have lessened environmental stress, allowing larger sizes to be achieved in the *E. lacustris* population. Although prevention of genotypic expression in the phenotype due to environmental stress is difficult to prove in the fossil record, especially in populations separated by a substantial period of time, it is common in many extant animals where limited resources may prevent full size being achieved.

Alternatively, if *Eurypterus* chose to mate and moult *en masse* in the brackish or euryhaline settings where they lived, rather than venture into the more physiologically stressful hypersaline settings represented within the Bertie Group, several pieces of evidence point towards them doing so in close proximity to such an environment. (Indeed, with their general sites of habitation moving from marine and euryhaline settings to entirely non-marine over the course of eurypterid evolution [Plotnick, 1999], a specific preference towards hypersaline environments, unless for brief excursions, seems unlikely). The lack of carcasses or bioturbation in beds containing *Eurypterus* exuviae in the Bertie Group indicates firstly that predation, more likely to occur in a lower, normal salinity environment, happened elsewhere, and secondly, that exuvial burial took place in an environment unsuitable for bioturbators (i.e. one that was hypersaline). Furthermore, the excellent preservation of the cuticle itself may

be a result of the environment it was buried in. Hypersaline environments have been shown to be sites of excellent preservation due to the lack of chitinoclastic bacteria (Mutel et al., 2008). Thus, the dearth of carcasses amongst the moults and presence of many fully articulated specimens suggests that if shed exuviae were transported from the moulting/mating grounds in lower salinity, estuary-like settings into nearby hypersaline, lagoon-like environments following ecdysis, overall chances of preservation would have been greatly increased. The lack of apparent sorting and presence of all life stages in this study would indicate proximity of the site of ecdysis to burial. Under these circumstances, the abundant accumulations of eurypterids in only the Phelps Waterlime Member of the Fiddlers Green Formation and A Member of the Williamsville Formations may be the result of taphonomic windows, rather than solely from time-averaging, with environmental conditions aligning briefly to allow for excellent preservation of shed exuviae (as a result of deposition in a hypersaline environment). That eurypterid specimens from other formations within the Bertie Group are generally rare, despite generally homogeneous facies, supports this hypothesis.

### 5.4. The mass-mate-spawn-moult hypothesis

Based on our results, a revised mass-mate-spawn-moult hypothesis is proposed herein. Following mating, males left the breeding area to return to deeper waters (where they moulted), whilst females remained behind to fertilise their eggs. Braddy and Dunlop (1997) suggested that female eurypterids could delay fertilisation of their eggs until environmental conditions were optimal using their horn organ. However, if the horn organ is shed during ecdysis, the female would not necessarily seek to moult until she had deposited her fertilised eggs. Thus, if females moulted shortly after depositing their eggs, this would leave the observed abundance of female moults. Conversely, if female eurypterids moulted more often, similar to *Limulus*, this may also explain the prevalence of female exuviae seen here.

An alternative explanation of gender bias within the mass-mate-spawn-moult hypothesis lies in interpretation of the genital appendage. If specimens with the type A genital appendage are actually males, as suggested by Kamenz et al. (2009), the results would suggest more *Limulus*-like mating behaviour, with more males competing for fewer females at the breeding site. In this alternative scenario, females would remain in deeper waters, only coming into shallower water to breed, whilst males would remain closer to shore, in greater abundance, until they mated successfully. A larger number of male moults would result.

It will always remain difficult to prove complex aspects of the life cycle of an extinct animal. Empirical analysis of fossil populations and analogues with extant taxa remain the only ready test for such hypotheses. The revised mass-mate-spawn-moult hypothesis presented herein is consistent with several independent lines of evidence and provides a model for future work, particularly in regards to arthropod moult assemblages and eurypterid autoecology.

## 6. Conclusions

1. The majority of eurypterid specimens in the Bertie Group represent moulted exuviae that have undergone limited tidal transport. The presence of many whole specimens indicates a generally calm depositional environment relatively close to the site where ecdysis took place.
2. Adult eurypterids may have preferentially chosen calm, predator-free hypersaline environments to mate and moult. Alternatively, if moulting and mating did not take place specifically in hypersaline environments, they did so relatively near to such settings. The eurypterid-rich beds of the Bertie Group may represent taphonomic windows, rather than solely time-averaged assemblages, where a

- proximity to hypersaline environments allowed for brief but excellent preservation of mass accumulations of shed exuviae.
- Specimens from the Fiddlers Green Formation (e.g. *E. remipes*) are, on average, smaller than those from the Williamsville Formation (e.g. *E. lacustris*), however there was little difference in the minimum and maximum sizes present. Differences in juvenile and adult size-frequency distributions between *E. remipes* from the Fiddlers Green Formation and *E. lacustris* from the Williamsville Formation are interpreted as indication of the depositional setting of each formation: the former shallower; the latter deeper.
  - The mass-moult-mate hypothesis is re-interpreted as the mass-mate-spawn-moult hypothesis in light of the abundance of females and the predominance of larger adult specimens (based on current genital appendage gender determination). According to this new hypothesis, males and females would have gathered at a specific breeding site, similar to *Limulus*. Following mating, males left the area and females remained, delaying fertilisation until conditions were optimal for spawning, then moulted before returning to deeper waters.
  - Similar to *Limulus*, females remained at the breeding site for a similar or shorter duration than males, but also moulted more often, thus leaving a predominance of female exuviae.
  - In the alternative Type A as male hypothesis, *E. remipes* and *E. lacustris* behaved similarly to *Limulus* at breeding sites, where a predominance of males competed for limited females, and females left the breeding ground once having mated. The abundance of male moults would therefore be due to a larger number of males moulting, before or after mating, near the breeding site.

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