

Geological context, biostratigraphy and systematic revision of late early Cambrian olenelloid trilobites from the Parker and Monkton formations, northwestern Vermont, U.S.A.

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In northwestern Vermont, upper lower Cambrian (Dyeran Stage) dysoxic deposits of the Franklin Basin are separated by 7 km from coeval, shallow-shelf deposits of the Monkton Formation on the Middlebury platform. This report presents a systematic revision of olenelloid trilobites from three localities within the basal facies of the Parker Formation (including the Parker quarry Lagerstätte) and three localities within the Monkton Formation. The study reveals a previously underestimated diversity of olenelloid species in both formations. *Olenellus agellus*, *O. crassimarginatus*, *O. transitans* and *O. aff. transitans* are presently known only from the basal facies; *Bolbolonellus hermani*, *B. cf. brevispinus* and several indeterminate olenelloid species are presently known only from the shelf facies; and *O. thompsoni*, *O. aff. fowleri* and *Mesonacis vermontanus* occur in both facies. The revisions demonstrate that (1) the Parker and Monkton formations share several species, thus strengthening previous claims for at least partial age-equivalence of the units; and (2) the regression(s) represented by the Monkton Formation began after the formation of the Franklin Basin but prior to the deposition of the Parker quarry Lagerstätte. Some newly documented elements of the Parker and Monkton formation faunas are possibly conspecific with olenelloids from Nevada, which permits a provisional correlation of the Parker quarry Lagerstätte with the *Bolbolonellus euryparia* Zone or overlying uppermost Dyeran *Nephrolonellus multinodus* Zone of the Laurentian Cordilleran margin. The Monkton Formation regression(s) were broadly contemporaneous with one or more of the four late Dyeran shallowing-up events that have been identified in the southwestern United States. This indicates that the regression(s) were a eustatic rather than an epeirogenically controlled phenomenon.

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STUDY of the spectacularly preserved early Cambrian fossils from the Parker Formation at Noah Parker's quarry in northwestern Vermont (Fig. 1) dates back more than 150 years (Hall 1859a), and the Parker quarry Lagerstätte (PQL) fauna continues to yield valuable insights into early animal evolution (e.g., Conway Morris & Caron 2014). The site is well known for its preservation of a diverse assemblage of trace fossils, sponges, brachiopods, non-mineralised organisms and trilobites (e.g., Resser & Howell 1938; Shaw 1954, 1955; Rigby 1987; Whittington 1989; Lieberman 1998, 1999; Webster 2009a; Conway Morris & Caron 2014; this report). However, despite its importance and long history of study, much fundamental systematic and biostratigraphic work remains to be done on the PQL and on the Parker Formation in general.

Many elements of the PQL fauna are in need of modern systematic treatment. With few exceptions (e.g., *Bathynotus holopygus* [Hall 1859a]; Webster 2009a), non-olenelloid trilobites from the site have received essentially no attention for more than 60 years (Resser & Howell 1938; Shaw 1955). The olenelloid trilobites have been periodically studied over the last few decades in efforts to clarify the taxonomy and phylogeny of the group (e.g., Whittington 1989; Lieberman

1998, 1999), but even these relatively recent systematic treatments are in need of revision. Solid alpha taxonomy is a prerequisite for production of robust hypotheses of evolutionary relationships and biostratigraphic correlation (see below).

The age of the PQL is poorly constrained in comparison to the tight biostratigraphic control on the age of lower Cambrian Lagerstätten in the southwestern United States (e.g., the Ruin Wash Lagerstätte; Webster *et al.* 2008). A high-resolution, species-level biostratigraphic zonation has not been developed for the Waucoban Series (traditional trilobite-bearing “lower Cambrian” of Laurentia; Palmer 1998a) in the northern Appalachian region. Construction of such a zonation is hindered by the geological complexity of the region (Clark 1936; Schuchert 1937; Cady 1945; Booth 1950; Shaw 1958; Stone & Dennis 1964; Dorsey *et al.* 1983; Mehrtens & Dorsey 1987; Mehrtens & Borre 1989; Mehrtens & Hadley 1995; Ratcliffe *et al.* 2011), the fact that most exposures span very limited stratigraphic thicknesses and often lack trilobites or yield only poorly preserved specimens, and the aforementioned need for modern systematic revision of the faunas.

Waucoban biostratigraphy is based primarily on

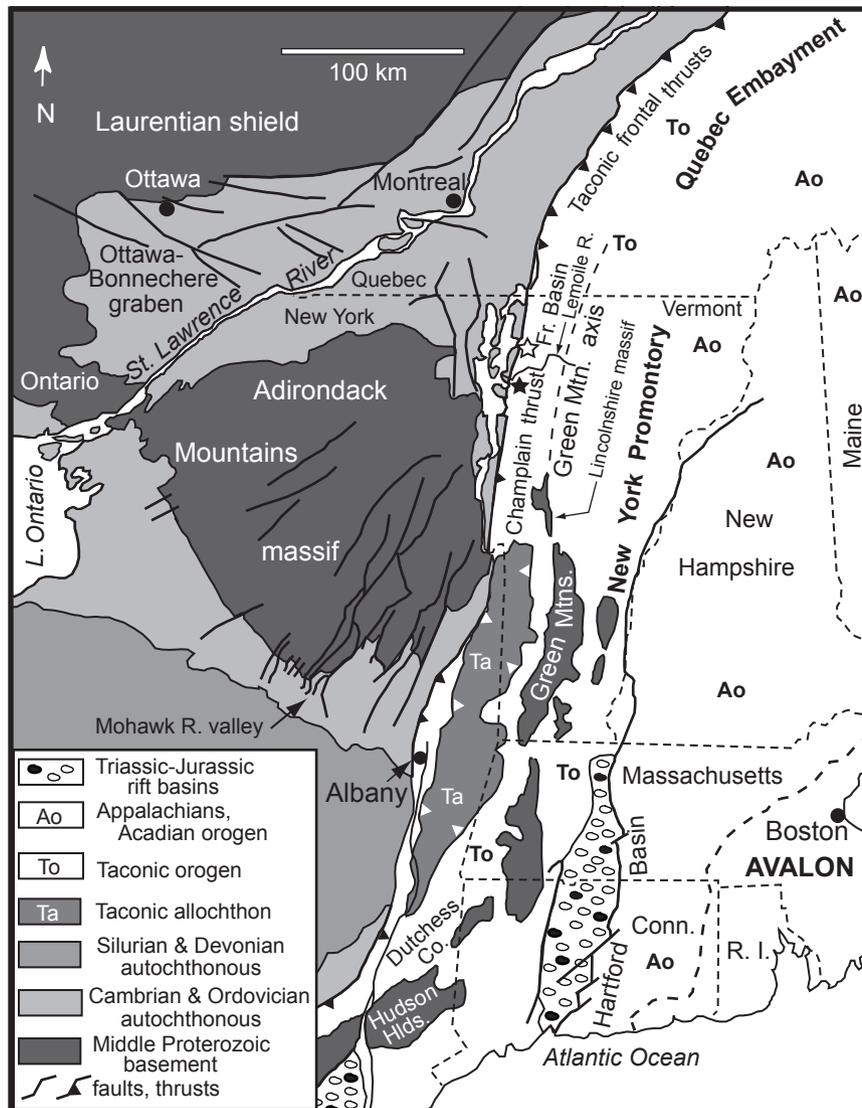


Figure 1. The Parker quarry (lower Parker Formation, white star, approximate coordinates N 44° 44.541', W 073° 09.423') and Powerline section (middle Monkton Formation, black star, Figs 3, 4) studied in this report in the context of regional geology. Dysoxic Franklin Basin extends from Lemoille River into southern Quebec. Figure shows Iapetan rift-related features: the Quebec Embayment and New York Promontory rift segments and the intracratonic, transform-parallel or failed arm of the Ottawa–Bonnechere graben. Modified from Hayman & Kidd (2002, fig. 1) and Landing (2007, fig. 1). Abbreviations: Ao, areas accreted to Laurentia in Acadian orogeny; Hlds., Highlands; Fr. Basin, Franklin Basin, Ta, Taconic allochthon; To, Taconic orogen.

trilobites (e.g., Palmer 1998a; Hollingsworth 2011; Webster 2011a; Webster & Bohach 2014). Of the PQL trilobites that have been studied in recent decades, the vast majority are known only from northwestern Vermont and are therefore of no use in correlation to other regions of Laurentia where biostratigraphic zonation is better developed (e.g., the southwestern United States; Webster 2011a). One olenelloid species—*Olenellus crassimarginatus* Walcott 1910—also occurs in the Kinzers Formation of Pennsylvania (Lieberman 1999; herein), but a species-level biostratigraphic zonation is also lacking in that poorly exposed region. Some non-olenelloid trilobites from the PQL such as *Bathynotus holopygus* and *Kootenia marcoui* (Whitfield 1884) do occur elsewhere and indicate a late but not latest Dyeran age (the upper stage of the two-stage Waucoban series; Webster 2009a), but a more precise age determination for the PQL has proven difficult to obtain. Pending modern systematic study, even local correlations—such as the supposed age-equivalence of the Waucoban portion of the Parker Formation and at least a portion of the adjacent Monkton Formation of northwestern and west-central Vermont (Figs 1, 2; Appendix 1; Cady 1945; Shaw 1954, 1958, 1962; but see Ratcliffe *et al.* 2011 who assigned the entire Monkton Formation to the “middle Cambrian” [discussed below])—should be considered tentative if they

are based on purported species-level similarity in trilobite faunas.

This paper presents a systematic revision of olenelloid trilobites from the PQL and two other localities in the Parker Formation, based on detailed examination of more than 70 specimens, many of which have not been previously studied (Appendix 2). Olenelloids from three localities within the Monkton Formation are also described, based in part on newly collected material from what is herein designated the “Powerline section” (Fig. 1; documented herein). A revision of non-olenelloid trilobites from these units will be published elsewhere.

Modern taxonomic procedures are applied to the olenelloid trilobites in order to (1) test the hypothesis of age-equivalence between the lower Parker Formation and the middle Monkton Formation and (2) develop provisional constraints on the correlation of the PQL and Powerline section with the biostratigraphic framework of the Cordilleran margin of Laurentia. Development of firmer age constraints on horizons within the Parker Formation (including the PQL) and in the Monkton Formation (including the Powerline section) refines our understanding of the structural history of the eastern margin of Laurentia during the Cambrian and helps place it in broader geologic context. For example, improved biostratigraphic data

into a passive-margin shelf. Marine transgression over this shelf is recorded by the upper Pinnacle Formation and lenticular carbonates (e.g., White Brook Dolostone) and regionally extensive, pyritic black mudstones (e.g., Fairfield Pond and Moosalamoo formations) in the overthrusts of the Champlain slice (Figs 1, 2). The oldest highly fossiliferous units include sandstones of the Cheshire Formation that have yielded fragmentary olenelloids, and low diversity Dyeran faunas occur in the dolostone-dominated Dunham Formation (Shaw 1954, 1955, 1958, the Cheshire Formation is his “Gilman Quartzite”; Mehrtens & Gregory 1984; Fig. 2). The fossils studied herein constrain the timing of events during the subsequent Dyeran evolution of this shelf.

Parker Formation of the Franklin Basin

Parautochthonous Cambrian–Ordovician shelf carbonates and sandstones of the Middlebury synclinorium lie just east of the Champlain thrust (Fig. 1). This shallow-shelf succession is abruptly replaced along strike by coeval dysoxic/anoxic mudstone- and debris flow-dominated facies of the St. Albans synclinorium (Figs 1, 2). Shaw (1958) referred this mudstone succession—including the Parker Formation—to a “Franklin Basin” that extends from the Lemoille River northwards into southern Quebec (Fig. 1; Mehrtens & Dorsey [1987] referred this same mudstone-dominated basin succession to a “St. Albans Reentrant”, although “reentrant” traditionally indicates much a larger recess of a rifted continental margin [e.g., Thomas 1977]). Landing (1983, 2007, 2012; see also Landing *et al.* 2007, 2009) emphasised that the black mudstones of the Franklin Basin record long-term (Dyeran–Middle Ordovician) dysoxia on the upper continental slope with depths of no more than 100 m.

Massive, carbonate clast/arenaceous conglomerates are interbedded with Franklin Basin mudstones and also abut, and even overlie the Middlebury shelf succession (Stone & Dennis 1964). These relationships led Rogers (1968) to conclude that the abrupt transition from the shelf to the Franklin Basin in northwest Vermont (Fig. 2) was one of the few places in eastern North America where the early Palaeozoic shelf margin is preserved and was not disrupted by Ordovician (Taconian) and later orogeny. Mehrtens & Dorsey (1987; also Mehrtens & Borre 1989) invoked syndepositional faulting to explain the development and maintenance of the shelf-to-basin transition in the vicinity of the Lemoille River (see Mehrtens & Dorsey [1987] for a review of older interpretations). Extending that model, Landing *et al.* (2007, 2009) linked the formation of the eastern terminus of the Ottawa-Bonnechere graben in northern New York and Quebec to rejuvenation in the late early Cambrian of on-strike faulting that defined the southern margin of the Franklin Basin by fracturing the east margin of Laurentia and by abrupt subsidence of the west Vermont—northeastern New York shelf. A debris apron that extends at least 30 km north of the Lemoille River lies at the contact of the Dunham and Parker formations (Fig. 2). This debris apron suggests the proposed faulting that defined the southern margin of the Franklin Basin was abrupt because mass movement of poorly consolidated Dunham Formation sediment is locally preserved at the Dunham–Parker transition (MW & EL unpublished data).

Formation of the Franklin Basin was initiated during the late early Cambrian. The black mudstones of the lower Parker Formation contain a Dyeran fauna (Walcott 1886, 1890b; Shaw 1954) and overlie dolomitised shelf

carbonates of the Dunham Formation that also contain Dyeran faunas (discussed above). Shaw (1954, 1958, 1962) tentatively correlated the Dyeran faunas of the basal Parker Formation and platformal Monkton Formation (discussed below) which, if true, means that the Franklin Basin and Middlebury shelf successions were differentiated in northwestern Vermont by the late Dyeran (Fig. 2). Shaw’s (1954, 1958, 1962) purported correlation is tested herein based on revised trilobite systematics.

Monkton Formation of the Middlebury Shelf

Many trilobites examined in this study come from the Monkton Formation and record the upper range of Dyeran faunas on the Middlebury shelf (Figs 1, 2). The Monkton Formation crops out at the southern margin of the Franklin Basin and is recognisable for about 70 km southwards into central Vermont (e.g., Ratcliffe *et al.* 2011). A south-to-north facies change from restricted marine, super- to sub-tidal deposits to more open marine conditions takes place within the unit in the Burlington area about 30 km south of the platform margin (Goldberg & Mehrtens 1998). The more open marine conditions are likely part of the explanation for the occurrence of trilobites at more northerly localities. Dyeran faunas with olenelloids have been reported at otherwise undescribed localities in the Burlington area (New York State Museum Paleontology Collection) and near Malletts Bay (Kindle & Tasch 1948; Tasch 1949; Speyer 1983; this report).

The Monkton Formation is part of a distinctive vertical facies transition on the shelf (Fig. 2) from grey, sandy dolostones of the Dunham Formation to overlying, frequently pink to red quartz arenites, dolomitic sandstones, and mudstones of the Monkton Formation. The upper Monkton Formation has a lithologically transitional contact with the lowest Winooski Formation dolostones (e.g., Stone & Dennis 1964; Fig. 2). Comparable carbonate–siliciclastic–carbonate shelf successions are exposed along the east Laurentian shelf from western Newfoundland to Georgia, with the transition into siliciclastic units such as the Monkton Formation regarded as marking the onset of the Hawke Bay regression during the late Dyeran (Palmer & James 1979; Lavoie *et al.* 2003; Landing *et al.* 2006, 2007, 2009). The presence of Monkton Formation clasts in the Rugg Brook Formation (unpublished work cited by Mehrtens & Hadley [1995] and Goldberg & Mehrtens [1998]) suggests that at least the upper portion of the Monkton Formation may be younger than the lower Parker Formation, and thus younger than the faulting that led to formation of the Franklin Basin (Fig. 2).

A more complex sequence stratigraphic interpretation of the Monkton Formation was proposed by Goldberg & Mehrtens (1998). They claimed that a karstified, eroded contact exists between the Dunham and Monkton formations near the southern limit of the Monkton Formation outcrop belt from Addison to Salisbury, west-central Vermont. By their interpretation, local, apparently epeirogenically driven, sea-level fall led to erosion of the Dunham Formation, followed by widespread non-marine deposition of the lowest Monkton Formation, and then deposition of the rest of the Monkton Formation as a transgressive systems tract. The Vermont Geologic Map (Ratcliffe *et al.* 2011) shows this Dunham–Monkton unconformity, but field checking by EL revealed only a sharp, non-karstific Dunham Dolostone–basal Monkton white sandstone contact at Ethan’s Cliff and, disturbingly, confirmed the

assertion of Goldberg & Mehrtens (1998, p. 22) that an 80 m covered interval without Monkton outcrops succeeds the highest Dunham exposure at Crane and Salisbury hills. Thus, there remains some ambiguity as to whether the Monkton Formation represents a regressive lithosome or a more complex lowstand-to-highstand systems tract between the Dunham and Winooski formation carbonates (see also the “Implications for correlation” section, below).

LOCALITIES

Olenelloid trilobite specimens are here described from six localities: three in the Parker Formation (Parker quarry, Kelly quarry and Locality 4789), and three in the Monkton Formation (Powerline section, Locality M-WC-1 and Colchester). Stratigraphic thicknesses are given in metres; thicknesses in feet as quoted in older literature have been converted. The faunal lists are based on the results of the systematic revisions that are presented in the “Systematic palaeontology” section.

Parker quarry

Lithology and stratigraphic provenance of the fossils.

Trilobites were first discovered at the Parker quarry on the west limb of the St. Alban’s synclorium in 1855 by Noah E. Parker while quarrying slate for flooring (Marcou 1888). Subsequent description of the fossils by Hall (1859a) sparked great interest in the geology and palaeontology of the region. The site was consequently visited by many researchers, including Jules Marcou and Charles Walcott (Walcott 1885, 1886; reviewed by Marcou 1888; Schuchert 1937).

Unfortunately the Parker quarry no longer exists; it was quarried away and overgrown over the years, with even relatively early reports (e.g., Schuchert 1937) not recording an actual examination of the quarry or a collection of new fossils. No evidence of the quarry was found during recent fieldwork in the area by EL. Modern field investigation of the site is therefore impossible. However, several early publications comment upon its location and lithological composition. As is often the case, such historical documentation contains ambiguity and inconsistencies (highlighted below where appropriate), and the following summary should be interpreted with caution.

The Parker quarry was located on the west side of Parker’s Cobble, a small but prominent hill in an area of generally low-lying farmland immediately west of the intersection of Georgia Middle Road and Reynolds Road, Franklin County (Fig. 1; see Shaw 1954, fig. 1 and Rigby 1987, fig. 1.1 for more detailed maps). Marcou (1880, p. 24; 1888, p. 113, pl. 13, fig. 1) provided geological details of the area of Parker’s Cobble, some aspects of which were corrected by Walcott (1886, p. 17, 18; 1890b, p. 533). The summit of the Cobble was approximately 15 m high. The lower two-thirds or so of the Parker quarry consisted of black slate (commonly called a “shale” [Walcott 1886] but with cleavage parallel to bedding [EL unpublished data]) within which trilobites were very rare, although several specimens were recovered from a greyer interval in the middle third of the quarry face (Marcou 1880, p. 24; 1888, pl. 13, fig. 1). Near the top of the quarry, the shale became sandy and slightly calcareous, and it was in this interval that most of the trilobite specimens were found. Above the trilobite zone and supposedly forming the topographic break at the top of the quarry face was approximately two or three more metres of shale, above which was a lens of more resistant calcareous sandstone that capped the Cobble

and ran down its eastern flank (Marcou 1880, p. 24; Walcott 1886, p. 17, 18; Walcott 1890b, p. 533; Marcou 1888, p. 108, 113). The Cobble-capping unit is further discussed below.

Walcott (1910, 1912a) assigned three USNM locality numbers to fossil collections from the Parker quarry. One of these, USNM Locality 319g, was described as “shales at Parker’s Quarry” (Walcott 1912a, p. 250). Material labelled as coming from this locality included the trilobites figured by Whitfield (1884), which had apparently been collected by Marcou (Whitfield 1884, p. 139, 151; Marcou 1888, p. 127). A second locality, USNM Locality 319m, was described as “shales of No. 6 of the section at Parker’s Quarry” (Walcott 1912a, p. 251). This is a reference to the measured section presented by Walcott (1886, p. 15–17; 1890b, p. 552–554), which included the Parker quarry. USNM Locality 319m is therefore apparently exactly equivalent to USNM Locality 319g (a conclusion also reached by Shaw 1954, p. 1040).

The third USNM locality number associated with the Parker quarry is USNM Locality 25. Walcott (1910) described USNM Locality 25 as “in the argillaceous shales of Parkers quarry” (p. 339) and as “dark, siliceous shales at Parkers quarry” (p. 310, 341). Later, he described it as “sandstone just above Parker’s Quarry” (Walcott 1912a, p. 188). Shaw (1954, p. 1040) believed that this locality “certainly refers to the arenaceous dolomite or dolomitic sandstone that caps Parker’s Cobble and extends down the eastern slope”, which would mean that the fauna came from the interval above the quarry rather than from the quarry itself. Shaw’s (1954) interpretation is (perhaps) consistent with the description of USNM Locality 25 provided by Walcott (1912a), but is inconsistent with the description provided by Walcott (1910). It is therefore possible that Shaw’s (1954) assignment of USNM Locality 25 to the Cobble-capping unit was erroneous, and that USNM Locality 25 referred to the sandy, calcareous shale that formed the upper portion of the quarry face, and lay stratigraphically above the darker, more slaty and less fossiliferous interval midway up the quarry and stratigraphically below the Cobble-capping unit. The precise provenance of USNM Locality 25 will likely never be resolved. The most serious effect of this ambiguity is that it creates uncertainty as to the thickness of the stratigraphic interval represented by the Parker quarry Lagerstätte (PQL) faunal assemblage, as now discussed.

Given the identical nature of USNM Locality 319g and USNM Locality 319m, and the fact that previous workers were inconsistent in their distinction of USNM Locality 25 from USNM Locality 319m—to the extent that Shaw (1954, p. 1041) commented that “for all practical purposes the listed faunas for Localities 25 and 319m must be regarded as inextricably mixed”—it is necessary to pool all specimens from these three collections into a single assemblage. But what is the thickness of the stratigraphic interval represented by this pooled assemblage? From Marcou’s (1880, 1888) illustrations and descriptions, it seems probable that the majority of the trilobites from the Parker quarry were recovered from an interval of approximately 8 to 10 m in stratigraphic thickness that spanned the upper two-thirds of the quarry, with a slaty lower portion and a sandier, calcareous upper portion. Such an estimate is consistent with the figures presented by Shaw (1954, p. 1040), who believed that 15 m of shale were present on the west flank of Parker’s Cobble and that the fossils from the Parker quarry were collected from near

the middle of that interval. This 8 to 10 m stratigraphic interval would surely incorporate Walcott's (1910, 1912a) USNM Locality 319g and USNM Locality 319m. If USNM Locality 25 referred to the sandier upper portion of the quarry, then this would also be included within the same 8-10 m thick interval.

However, if USNM Locality 25 referred to the Cobble-capping unit, then the PQL faunal assemblage would have been pooled from a much thicker stratigraphic interval in the lower Parker Formation. Schuchert (1937, p. 1025) noted that the sandy, calcareous unit that capped Parker's Cobble was approximately 9.1 m thick, whereas Shaw (1954, p. 1040) suggested a thickness of 12.2 m (such a difference might be attributable to exactly where the thickness estimate was taken on a probably lenticular unit). If USNM Locality 25 does refer to the Cobble-capping unit, then—using the estimates of stratigraphic thickness provided by Shaw (1954, p. 1040)—the pooled collections of USNM Locality 319g, USNM Locality 319m, and USNM Locality 25 probably incorporate a stratigraphic thickness of at least 18.3 m and perhaps as much as approximately 27.4 m.

Stratigraphic position within the Parker Formation.

Several authors have estimated the position of the Parker quarry within the Parker Formation. Small-scale faulting with displacements of up to several metres is rife within the formation (Stone & Dennis 1964, p. 65; EL & MW personal observations), and estimates of stratigraphic position within the formation of particular outcrops should not be considered precise. However, Walcott (1886, fig. 1) actually collected in the Parker quarry, and his generalised stratigraphic interval for the quarry as low within the Parker Formation (i.e., somewhere in the lower 65 m of strata that compose his "unit 6" that lies immediately above the prominent contact with the Dunham Formation) is certainly valid.

Schuchert (1937, p. 1013) estimated that the Parker quarry was approximately 38.1 m above the massive "Mallet Dolomite" (= sandy, uppermost Dunham Formation). Shaw (1954, p. 1040) estimated the shale in the Parker quarry to lie between 36.6 m and 51.8 m above the base of the Parker Formation, and probably near the middle of this interval; an estimate of 45.7 m was subsequently offered by Shaw (1955, p. 778). The lenticular, sandy, calcareous unit said to form the cap and eastern flank of Parker's Cobble was estimated to lie 51.8 to 64 m above the base of the Parker Formation (Shaw 1954; the top of this dolomitic unit had previously been estimated to lie 61 m above the base of the Parker Formation by Walcott 1886).

The position of the Parker quarry and this Cobble-capping unit relative to the Dyeran-Delamaran boundary (i.e., base of the Laurentian "middle Cambrian") is not well constrained. Dyeran fossils have been recovered from a (likely turbiditic; Landing *et al.* 2007) limestone within the Parker Formation at a quarry on the old Hall Farm (USNM locality 25a; Walcott 1912a; Shaw 1954). Shaw (1954, p. 1042) estimated this limestone to lie approximately 137.1 m above the base of the Parker Formation. Based on that estimate, he considered USNM Locality 25a to be the stratigraphically highest local occurrence of olenelloids, and depicted it as lying approximately 73 m stratigraphically above the dolomitic cap of Parker's Cobble (Shaw 1954, fig. 3). However, he also acknowledged considerable uncertainty in the stratigraphic location of USNM Locality 25a, stating that it could lie as much as 61 m lower than

the depicted position (Shaw 1954, p. 1042). Within those bounds of uncertainty, USNM Locality 25a could be stratigraphically separated from the fossil beds of the Parker quarry by as little as 12 m or so. Given the structural complexity of the region, the supposed stratigraphic (and thus age) separation between the Parker quarry and USNM Locality 25a should not be uncritically accepted. The fauna of USNM Locality 25a has yet to receive modern systematic treatment, but the list provided by Shaw (1954, p. 1042) suggests partial compositional differences with the Parker quarry fauna. Such compositional differences, if true, could be attributable to a difference in lithofacies (carbonate turbidite versus siliciclastic mudstone) and/or age.

Strata estimated to lie approximately 176.8 m above the base of the Parker Formation (and therefore approximately 112.8 m above the top of the dolomitic cap of Parker's Cobble) were considered by Shaw (1954, 1957a, 1958) to be probably "middle Cambrian" (= Delamaran Stage of current usage) in age. However, this age assignment was based on the absence of olenelloid trilobites rather than the presence of any definitively Delamaran taxa, and must be considered equivocal. Indeed, the stratigraphically lowest trilobite indicative of a Delamaran age appears to be a form identified by Shaw (1954, 1957a) as *Mexicella stator* (Walcott 1916a) from Shaw's (1954, 1957a) locality SA-EC-1, which he estimated as lying approximately 192 m above the dolomitic cap of Parker's Cobble (Shaw 1954, fig. 3). Palmer (1971) suggested that Shaw's (1954, 1957a) *Mexicella stator* was misidentified and probably represents a species of *Semisphaerocephalus* Ivshin 1953, which would indicate a younger "late middle Cambrian" age. Irrespective, earlier Delamaran faunas have yet to be sampled from the Parker Formation. The Dyeran-Delamaran boundary must lie within the Parker Formation, but its precise horizon is poorly constrained.

Following Walcott (1886), most workers have interpreted the Cobble-capping dolomitic unit as a lenticular mass within the Parker Formation. However, Stone & Dennis (1964, p. 39, 70, fig. 4, plate 1) reinterpreted it as part of the Rugg Brook Dolomite, which is typically considered to be a "middle Cambrian" conglomeratic debris flow in erosional contact with the underlying Parker Formation (Schuchert 1937; Shaw 1958). Although not commented upon by Stone & Dennis (1964), their reassignment (had it been correct) had potential biostratigraphic implications because if the fossils from USNM Locality 25 were collected from this Cobble-capping unit (as suspected by Shaw 1954; see above) and if the Cobble-capping unit was part of the "middle Cambrian" Rugg Brook Dolomite (as claimed by Stone & Dennis 1964), then the Rugg Brook Formation would be olenelloid-bearing. This would mean that either (1) the Rugg Brook Formation was at least in part "lower Cambrian", or (2) olenelloids locally persisted into the "middle Cambrian".

However, the reassignment proposed by Stone & Dennis (1964) seems to have garnered little support from subsequent workers. For example, the western portion of the map presented by Dorsey *et al.* (1983, fig. 1)—despite being taken primarily from the work of Stone & Dennis (1964)—showed all of Parker's Cobble as contained within the Parker Formation; no comment was made by Dorsey *et al.* (1983) regarding this difference. Furthermore, the concept of the Rugg Brook Formation (= Rugg Brook Conglomerate; = Rugg Brook Dolomite)

has been considerably revised in recent decades. It was originally conceived as a discontinuously exposed but distinct conglomeratic unit at the base of the St. Albans Slate (Schuchert 1933, 1937; Howell 1939; Shaw 1958, 1962; Stone & Dennis 1964; Dorsey *et al.* 1983). It was subsequently redefined to consist of a series of discrete carbonate debris flows interbedded within the shale of the Parker Formation and the Skeels Corners Slates (Mehrtens & Dorsey 1987; Mehrtens & Borre 1989; Mehrtens & Hadley 1995) and thus was no longer considered to be a time-stratigraphic unit. In fact, the most recent geological map of Vermont does not recognise the Rugg Brook Formation at all, but instead assigns the various conglomerate lenses to highly localised, patchily developed members within the Parker Formation and the Skeels Corners Slate (Ratcliffe *et al.* 2011). The eastern slope of Parker's Cobble is now mapped as a calcareous sandy conglomerate member (conglomerate with dolostone and sandstone clasts in a shaly matrix) of the Parker Formation (Ratcliffe *et al.* 2011).

Trilobite fauna. The pooled assemblage representing the PQL fauna is fairly diverse, although comprehensive compilations are now many decades old (e.g., Shaw 1954, 1955) and many of the elements are in dire need of modern systematic treatment. Regarding trilobites from the site, Webster (2009a) presented a full redescription of *Bathynotus holopygus*, and the olenelloids are revised herein. Shaw (1954, 1955) also recognised the occurrence within the PQL fauna of the dorypygids *Bonnina capito* (Walcott 1916b), *Kootenia marcoui* and *Protypus hitchcocki* (Whitfield 1884); the eodiscid *Pagetides parkeri* (Walcott 1886); and the “ptychopariid” *Billingsaspis adamsii* (Billings 1861). These taxa are currently under study and will be the subjects of future papers.

A great many olenelloid species have been reported from the PQL over the years, including *Mesonacis vermontanus* (Hall 1859a), *Olenellus agellus* Resser & Howell 1938, *O. brachycephalus* (Emmons 1860a), *O. crassimarginatus*, *O. georgiensis* Resser & Howell 1938, *O. thompsoni* (Hall 1859a), *O. transitans* (Walcott 1910) and *Paedeumias perkinsi* Resser & Howell 1938. As did Lieberman (1999), we recognise five of those species as valid: *M. vermontanus*, *O. agellus*, *O. crassimarginatus*, *O. thompsoni* and *O. transitans* (below; Appendix 2). However, two additional olenelloid species—*O. aff. fowleri* Palmer 1998b and *O. aff. transitans*—are documented from the site for the first time (see “Systematic palaeontology” section; Appendix 2). Many other olenelloid specimens from the site are unidentifiable to the species level and are left in open nomenclature (Appendix 2).

Kelly quarry

Lithology and stratigraphic provenance of the fossils.

The Kelly quarry (now private property) was located approximately 4.8 km southeast of Swanton and approximately 16.4 km NNE of Parker's Cobble (see Schuchert [1937, fig. 1, locality XXI] and Shaw [1954, fig. 1, Locality SA-C-1] for maps). Schuchert (1937, p. 1035) stated that the quarry exposed less than 9.15 m of the Parker Formation, and was overlain by 3 to 4.5 m of rusty red-weathering calcareous slate that was in turn overlain by approximately 7.6 m of ridge-forming dolostone.

Shaw (1954, p. 1041) estimated that the highly fossiliferous black slate zone of the Kelly quarry was approximately 3 m thick. The overlying brown-weathering,

grey, nonarenaceous dolostone was stated to be locally thick, but most of the fossils were from the lower 1.5 m. Both Schuchert (1937) and Shaw (1954) presented separate faunal lists for the two intervals. The faunal list for each of the fossiliferous intervals from the Kelly quarry was therefore pooled from a much thinner stratigraphic interval than the pooled faunal list for the Parker quarry.

Stratigraphic position within the Parker Formation.

Shaw (1954, p. 1041) estimated that the highly fossiliferous black slate zone of the Kelly quarry was approximately 45.7 to 48.8 m above the base of the Parker Formation. The fossiliferous portion of the overlying nonarenaceous dolostone was stated to be approximately 48.8 to 50.3 m above the base of the Parker Formation (Shaw 1954). These estimates place the Kelly quarry at roughly the same stratigraphic distance above the base of the Parker Formation as the Parker quarry, although whether this represents evidence for time-equivalence of their faunas is unclear (this would require assumptions about basin floor topography and sedimentation rate).

Schuchert (1937, p. 1035) tentatively correlated the ridge-forming dolostone overlying the Kelly quarry with the dolostone “that makes the Cobble on the Parker farm” (presumably meaning the Cobble-capping unit). Shaw (1954, p. 1041) similarly believed that the Kelly quarry was correlative to the Parker quarry. However, field studies in recent decades have demonstrated that the numerous calcareous bodies within the Parker Formation may be extremely localised lenses that do not correlate from site to site (e.g., Mehrtens & Dorsey 1987; Mehrtens & Borre 1989; Mehrtens & Hadley 1995; Ratcliffe *et al.* 2011). Such findings may undermine the utility of lithological similarity as a means of correlation between the Kelly quarry and the Parker quarry. In the absence of a detailed lithostratigraphic, sequence stratigraphic, or chemostratigraphic framework for the region, any proposed correlation between the quarries at this time must be based on palaeontological data.

Trilobite fauna. Fossils were reported from the Kelly quarry at least as early as 1906 (Schuchert 1937), and Shaw (1954, p. 1041) described the site as being highly fossiliferous. The Kelly quarry has yielded a rich trilobite fauna. Schuchert (1937, p. 1035) noted *Mesonacis vermontanus* in the lower part of the quarry, and “*Ptychoparella adamsi*, *Acrocephalites ? vulcanus*, and *Microdiscus*” (Schuchert 1937, p. 1035) higher in the quarry. The calcareous slates overlying the quarry yielded trilobite fragments that Schuchert (1937, p. 1035) attributed to *Olenoides marcoui* and *Olenellus thompsoni* along with hyolith and brachiopod remains. Shaw (1954, p. 1041; 1962, p. 337) listed a trilobite fauna from the slates of the quarry consisting of *Kootenia marcoui*, *Bathynotus holopygus?*, *Olenellus brachycephalus*, *O. [now Mesonacis] vermontanus*, *O. sp. indet.*, *Pagetides parkeri*, *Prozacanthoides sp. indet.*, *Ptychoparella teucer* Billings 1861 and *Periomma gaspensis* Rasetti 1955. He also listed *Kootenia marcoui*, *Olenellus sp. indet.*, *Pagetides parkeri* and *Ptychoparella teucer* from the overlying dolostone.

Recent study has shown that the single pygidium tentatively identified as *Bathynotus holopygus?* by Shaw (1954; figured by Shaw 1955, pl. 73, fig. 5; specimen MCZ 5040) does not represent that genus (see Webster 2009a, p. 388). Other non-olenelloid trilobites from the slates of the Kelly quarry are still under investigation. One species of

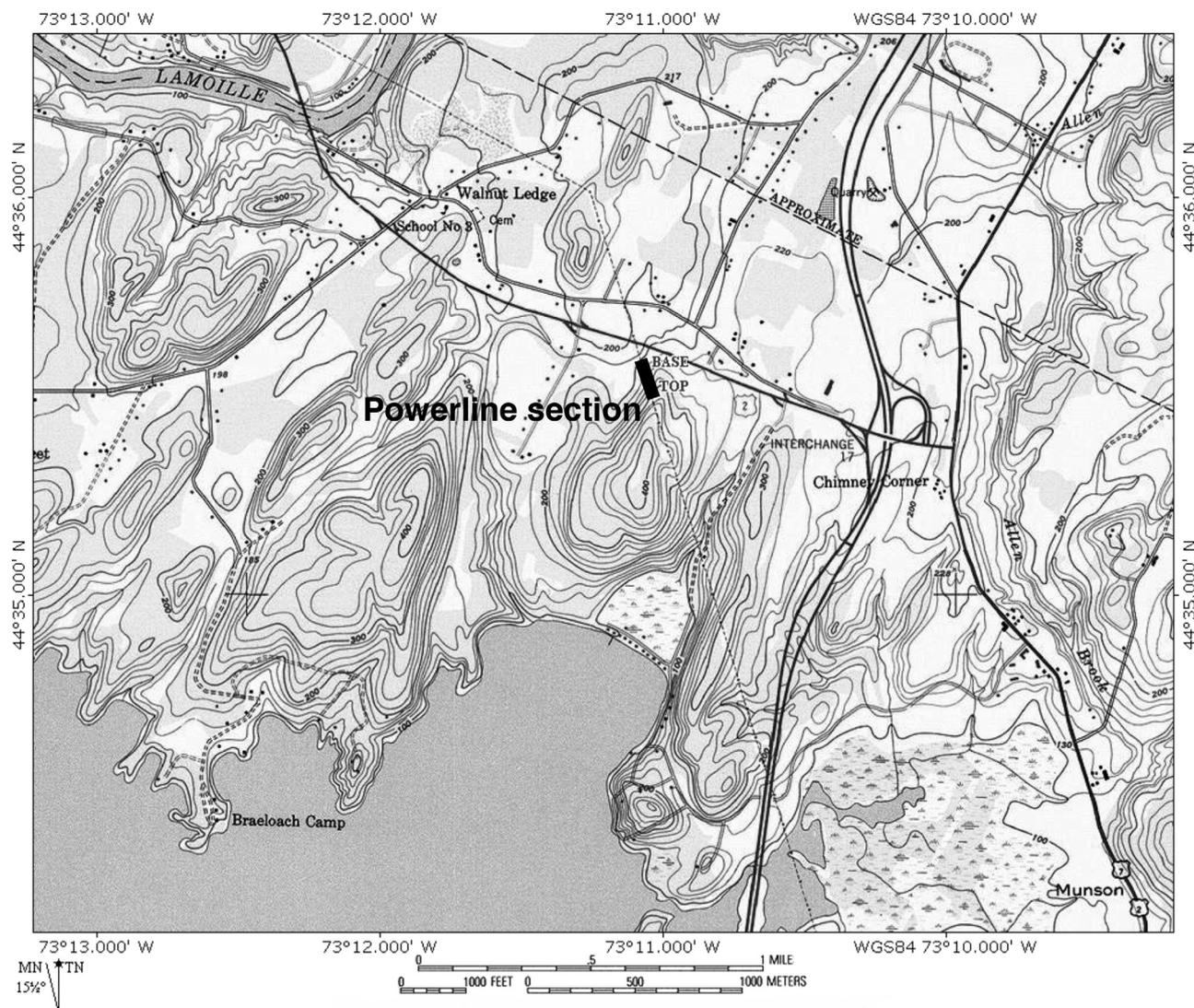


Figure 3. Map showing location of the Powerline section, described herein. Base of section N 44° 35.577', W 073° 11.065'. This hillside was also studied by Speyer (1983), and is likely the source for the fossils described by Kindle & Tasch (1948) and Shaw (1962, Locality M-WC-1). Map created with TOPO! software (© National Geographic, 2002).

olenelloid trilobite is here recognised in the Kelly quarry slate fauna: *Olenellus transitans*. Shaw (1954) reported six cephalons of *O. brachycephalus* from the Kelly quarry, and subsequently illustrated one (Shaw 1955, pl. 75, fig. 2; specimen MCZ 4994, later renumbered MCZ 108661; below; Appendix 2). This specimen represents *O. transitans* (as, presumably, do the other five).

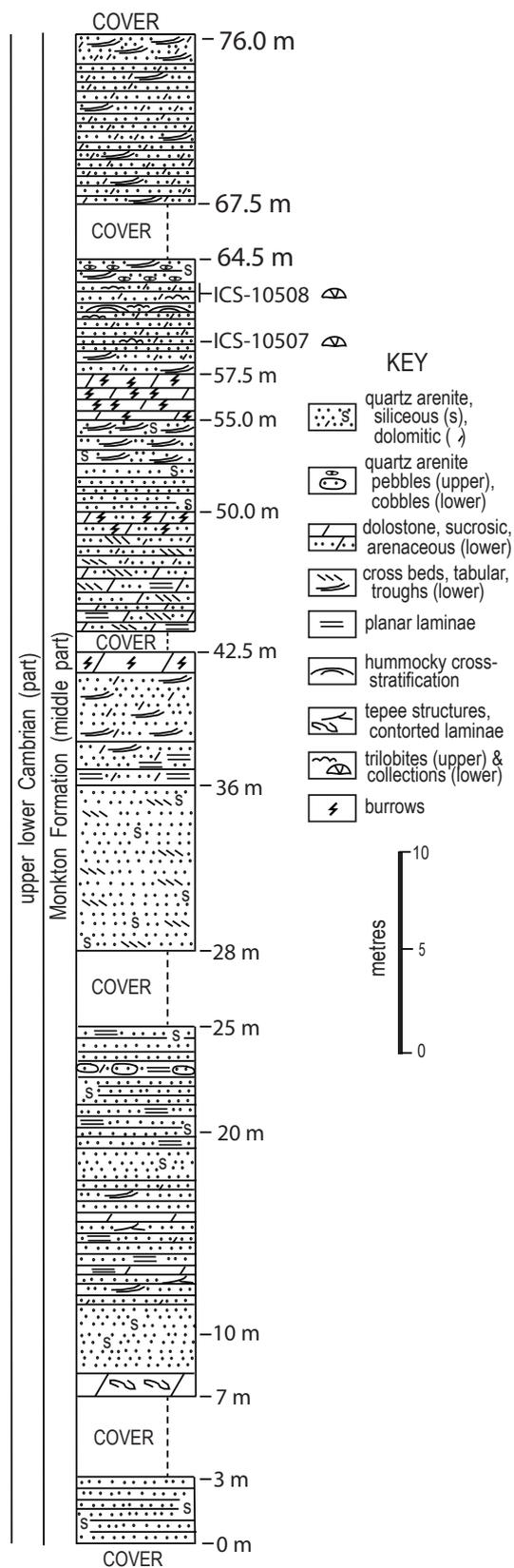
It is also possible that *Mesonacis vermontanus* occurs in the slates of the Kelly quarry. Schuchert's (1937, p. 1035) report of "an entire but uncollectable specimen of a small *Mesonacis vermontana*" in the lower part of the Kelly quarry cannot be confirmed, but given the distinctive form of this species it could be correct. Shaw (1954) also reported one glabella of *Olenellus* [now *M.*] *vermontanus* from the Kelly quarry (subsequently illustrated by Shaw 1955, pl. 75, fig. 10; specimen MCZ 4992, later renumbered MCZ 108662). This is a misidentification, however, and that specimen is herein treated as a fragment of an indeterminate olenelloid (see "Systematic palaeontology" section; Appendix 2).

Locality 4789

Lithology and stratigraphic provenance of the fossils. Two specimens from the MCZ were examined that were

labelled as coming from Locality 4789. However, the authors can find no mention of this locality in the literature, and its exact geographic and stratigraphic whereabouts remain unknown. Information cards with the two specimens state that Locality 4789 is "three miles south of Swanton". This locality is therefore in the vicinity of Swanton Junction, Franklin County. It is possible that this is another designation for the Kelly quarry (above), but unless this can be unambiguously demonstrated, Locality 4789 is best treated as a distinct locality. The two specimens examined herein are preserved as ochre-coloured (limonitic?) moulds in brown-weathering shale/siltstone. Each is preserved on a different slab, so the following faunal list is pooled over an unknown stratigraphic interval at this site in the Parker Formation.

Trilobite fauna. Two species of olenelloid trilobite are known from Locality 4789 (see "Systematic Palaeontology" section; Appendix 2): *Olenellus transitans* (known from one specimen [MCZ 52525, formerly labelled MCZ 2525]); and *O. agellus*? (a tentative identification based on a part and counterpart of a single individual [MCZ 193182 and MCZ 193183]).



Powerline section

Figure 4. Lithological details of the Powerline section in the middle Monkton Formation. Sample horizons that yielded trilobite collections are indicated with their collection numbers (ICS-10507 and ICS-10508).

Powerline section

Lithology and stratigraphic provenance of the fossils. The Powerline section (designation for this locality proposed in this report) in the Monkton Formation is currently exposed under high tension electrical lines. This north-facing, almost continuously exposed section crops out on the north side of a 100 m high knoll just north of Malletts Bay on Lake Champlain (Figs 1, 3). The base and top of the Monkton Formation are not exposed in the 76.1 m thick Powerline section (Fig. 4). Speyer (1983, fig. 3) measured a 67 m thick section on the same hillside. Observations made on the Powerline section generally corroborate Speyer’s (1983) conclusions that the section features intertidal to shallow subtidal facies, and only differ in some details. Although rhythmic or cyclic alternations are reported in Monkton Formation successions (Speyer 1983; Goldberg & Mehrtens 1998), such alternations are not obvious in the Powerline section (Fig. 4).

The Powerline section shows a generalised upward deepening, with a slight shallowing possibly represented at the top. Crenulated stromatolitic laminae and tepee structures are suggestive (but not necessarily diagnostic) of at least transient evaporitic conditions low in the section (below 18 m). Episodic higher energy conditions are marked by large intraclasts in a channel at 23 m, and trough cross-bedding appears above 12 m. These troughs have a north-south orientation through to the top of the section and are interpreted to record deposition in tidally dominated environments. The occurrence of abundant burrows in a dolostone bed (42 m) and in arenaceous dolostones (48.8–50 m) is consistent with a hypothesis of generalised deepening-upward/less restricted marine character of the depositional environments. The occurrence of lenses of comminuted trilobite sclerites (59–64 m, including new collections ICS-10507 [59 m] and ICS-10508 [62–64 m]) probably indicates the most normal marine, unrestricted environments, an interpretation consistent with a hummocky cross-stratified interval (60.1–60.4 m; see outcrop illustration by Speyer 1983, fig. 12A of “planar bedding”). Trough cross-bedded, dolomitic sandstones at 63.5–64.5 m and 74.5–76.1 m, with bedding plane exposures of north-south trending troughs at the top of the section, suggest a return to tidally dominated facies.

The Powerline section was deposited a relatively short distance south of the Franklin Basin–Middlebury shelf transition (Figs 1, 2). Its location is only 7 km from the southernmost outcrop of roughly coeval dysoxic mudstone of the lower Parker Formation (e.g., Stone & Dennis 1964, plate 1) and shows that very shallow, perhaps even restricted marine depositional conditions existed on the marginal parts of the northwest Vermont shelf.

Stratigraphic position within the Monkton Formation.

Given a 25° southeastward dip and exposure of the Dunham–Monkton contact in a Route 2 roadcut to the northwest (Stone & Dennis 1964), the base of the Powerline section is approximately 120 m above the base of the Monkton Formation. An unsuccessful attempt was made to recognise the Powerline section succession in an unweathered roadcut on Route 2 just northeast of the 100 m high knoll. In addition, a north-south trending vertical fault with indeterminate throw separates the west and east blocks of Monkton in the roadcut.

Thicknesses of the Monkton Formation along its outcrop belt are difficult to determine because the lower

and upper contacts of the unit are generally covered and its sections are often faulted. The Monkton's thickness has been estimated at 100 m or 150 m immediately north and east of Malletts Bay, respectively (Keith 1923, p. 108; Goldberg & Mehrrens 1998, p. 12). However, the estimate of 375 m by Stone & Dennis (1964) in this area is more accurate based on the outcrop pattern of the underlying Dunham Formation and overlying Winooski Formation. This means that the Powerline section exposes an interval approximately 120 m to approximately 196 m above the base of the Monkton Formation, and the faunas from the upper part of the Powerline section represent the middle of the Monkton Formation.

Trilobite fauna. The stratigraphically lower of the two collections (ICS-10507) contains *Olenellus thompsoni*, *Bolbolenellus* cf. *brevispinus* Palmer 1998b, *Bolbolenellus* sp. indet. and possibly olenelloid sp. indet. B (see "Systematic Palaeontology" section). The stratigraphically higher collection (ICS-10508) contains at least six olenelloid species: *O. thompsoni*, *O.* aff. *fowleri*, *O.* sp. indet. (a distinct form), *O.*? sp. indet. (a distinct form), olenelloid sp. indet. B and olenelloid sp. indet. C (below). "Ptychopariid" and dorypygid trilobites plus a small shelly fossil also occur in these collections and will be described elsewhere.

Locality M-WC-1

Lithology and stratigraphic provenance of the fossils. Kindle & Tasch (1948) described a fauna from the Monkton Formation that was collected from a hillside just north of Malletts Bay. This locality was subsequently named Locality I by Tasch (1949) and Locality M-WC-1 by Shaw (1962); the latter name is applied herein. The hand-drawn maps provided by Kindle & Tasch (1948, fig. 1) and Tasch (1949, fig. 1) show that Locality M-WC-1 likely corresponds to the Powerline section described above (Fig. 3). Stratigraphic and geographic proximity of these sites is further confirmed by the similarity of the olenelloid faunas and of fossil preservation between Locality M-WC-1 and ICS-10507 and ICS-10508. However, the stratigraphic interval over which the assemblage from Locality M-WC-1 was pooled is unknown, and it is herein treated as a distinct collection.

Stratigraphic position within the Monkton Formation.

The exact provenance of the collection described by Kindle & Tasch (1948) is uncertain based on an absence of stratigraphic data in that publication. For an unknown reason, Tasch (1949, p. 210) concluded that the material was from "near the bottom of the formation". Equally puzzling, Shaw (1954, p. 1044) estimated that the Kindle & Tasch (1948) collection came from 15 m to 30 m above the base of the Monkton Formation. Shaw (1958) later showed that the site that yielded the trilobites of Kindle & Tasch (1948) lies in the middle of the Monkton Formation outcrop belt. Perhaps more importantly, Speyer's (1983) report is in agreement with our conclusion that trilobites occur only in the upper part of the section on the 100 m high hill—a site which is in the middle of the Monkton Formation (discussed above). Later, Shaw (1962, p. 328) stated that the Kindle & Tasch (1948) collection was 125 m above the base of the formation as drawn by Stone (1951) or 34 m above the base of the formation as drawn by Cady (1945). Shaw's (1962) 125 m estimate of the stratigraphic position of the trilobite collection is the only estimate in

the earlier literature that approaches the actual stratigraphic range of observed trilobite debris in the Powerline section (184–189 m), as based on the geological map of Stone & Dennis (1964).

Trilobite fauna. A diverse trilobite and non-trilobite fauna has been reported from Locality M-WC-1 (Kindle & Tasch 1948; Tasch 1949; Shaw 1954, 1955, 1962). Non-olenelloid trilobite species reported from the site include *Billingsaspis adamsii*, *Antagmus typicalis* Resser 1937, *Bonnia capito*, *Prozacanthoides* sp. indet. and *Bonniella?* sp. (Kindle & Tasch 1948; Tasch 1949; Shaw 1954, 1955, 1962). These taxa are under revision and will be redescribed elsewhere. Kindle & Tasch (1948) recognised at least three species of olenelloid trilobites from the site (*Mesonacis vermontanus*, *Olenellus thompsoni* and *Bolbolenellus hermani* [Kindle & Tasch, 1948]), but Shaw (1954, 1962) recognised only two (*O. brachycephalus* and *B. hermani*). *Mesonacis vermontanus* and *B. hermani* are now confirmed to be represented (see "Systematic palaeontology" section). The fragmentary material figured by Kindle & Tasch (1948) as *O. thompsoni* might represent that species, but is herein conservatively treated as an indeterminate olenelloid.

Colchester

Lithology and stratigraphic provenance of the fossils.

The W. E. Crane collection housed at the NYSM contains four slabs of red-brown weathering, bioclastic, calcareous sandstone with moulds of trilobite sclerites. The precise provenance of this material is unknown—labels with the specimens state only that they were collected from "Colchester, Vermont". It is likely that they were sourced from a quarry in the Monkton Formation at Colchester, Chittenden County, just east of Malletts Bay. The provenance of the fossils within the quarry, and the stratigraphic position of the quarry within the Monkton Formation, is unknown.

Trilobite fauna. *Olenellus thompsoni* and olenelloid sp. indet. A have been identified within the collection (see "Systematic palaeontology" section). A "ptychopariid" also occurs and will be described elsewhere.

IMPLICATIONS FOR CORRELATION

Despite more than 150 years of work, the timing of many evolutionary and tectonostratigraphic events that took place in the northern Appalachians during the early Cambrian remains poorly constrained. A key factor in this haziness is the absence of a detailed Cambrian temporal framework for this region of Laurentia. Ideally, such a framework would integrate biostratigraphic, chemostratigraphic, geochronologic and chronostratigraphic data. The present paper deals exclusively with olenelloid trilobites and thus represents only one step towards construction of such an integrative framework, but nevertheless sheds light on several issues (below).

The following age constraints are based on species-level correlations. Biostratigraphic correlations of course come with caveats (e.g., Landing *et al.* 2013). However, detailed collecting of fossil-rich, mixed carbonate-siliciclastic Dyeran deposits of the southwestern United States has found that the stratigraphic range of any given olenelloid species within a single section is typically < 10 metres (Webster *et al.* 2003; Webster 2011a). Diachronism of observed species ranges among those sections (caused by, for example, facies tracking) is typically well below the resolution of detailed bio- and sequence stratigraphic zonation (see

range charts and discussion by Webster *et al.* [2003] and Webster [2011a]). Thus, although we do not claim that intervals from distinct localities that are correlated based on one or several shared species were necessarily deposited synchronously, we do consider it likely that those intervals share a closely similar depositional age.

Local correlation within the Parker Formation

Both Schuchert (1937) and Shaw (1954) considered the PQL and the Kelly quarry to be correlative. Their views were based on faunal similarity, lithostratigraphic similarity and/or similar estimated stratigraphic distance above the base of the Parker Formation. The now-outdated trilobite systematics used by those authors, and subsequent revisions to mapping (summarised above), necessitate re-examination of these putative correlations. Elements of the PQL olenelloid fauna are indeed shared with the Kelly quarry (*Olenellus transitans* and possibly *Mesonacis vermontanus*) and Locality 4789 (*O. transitans* and probably *O. agellus*). It is thus likely that, within the current limits of temporal resolution, the fossil-bearing intervals at these localities are correlative. If Locality 4789 is identical with the Kelly quarry (see above) then the case for age-equivalence of the PQL and the Kelly quarry would be further strengthened.

Local correlation to the Monkton Formation

Locality M-WC-1 was believed to be correlative with the Dyeran portion of the Parker Formation in general and with the “Kelly-Parker horizon” in particular (Shaw 1954, 1955, 1962). This conclusion was based, at least in part, on a shared trilobite fauna between Locality M-WC-1, the Parker quarry and the Kelly quarry. However, Ratcliffe *et al.* (2011) depicted the entire Monkton Formation as Delamaran in age, although this age assignment is inconsistent with the presence of olenelloids within the unit and with the longstanding assignment of this fauna to the “early” Cambrian (Kindle & Tasch 1948).

Elements of the PQL olenelloid fauna are shared with horizons within the Monkton Formation at the Powerline section (*Olenellus thompsoni* and *O. aff. fowleri*), Locality M-WC-1 (*Mesonacis vermontanus*) and Colchester (*O. thompsoni*). It is thus likely that, within the current limits of temporal resolution, the fossil-bearing intervals at these localities are indeed correlative. If Locality M-WC-1 is identical with one or both of the fossiliferous horizons at the Powerline section (as seems to be the case, see discussion above), then the case for age-equivalence of the PQL and that interval of the Monkton Formation would be further strengthened. This correlation provides biostratigraphic confirmation that the Franklin Basin and Middlebury Shelf successions were differentiated in northwestern Vermont by the late Dyeran. It also shows that the regression(s) represented by the Monkton Formation began after the formation of the Franklin Basin but prior to the deposition of the PQL in the basin.

Inter-regional correlation to the Kinzers Formation

Both the Parker Formation in the northern Appalachians and the Kinzers Formation of the central Appalachians span the upper Dyeran to the Delamaran (e.g., Shaw 1954, 1957a, 1958; Campbell 1971; Palmer 1971), and age-equivalence of at least some of their faunas is therefore to be expected. Precise correlation between particular localities within each of these units is difficult because limited exposure has hindered construction of a detailed local biostratigraphic

framework. Nevertheless, the occurrence of *Olenellus crassimarginatus* in the PQL of Vermont and at USNM Locality 8q and locality 22L in Pennsylvania suggests that these three localities are of similar age.

Provisional circum-continental correlation to the southwestern United States

The Appalachian and the Cordilleran margins of Laurentia share extremely few, if any, Dyeran trilobite species. Palmer (1964) suggested that fragmentary trilobite cephalae from the upper Harkless Formation (= lower Saline Valley Formation) of Nevada might be conspecific with *Wanneria walcottana* (Wanner 1901) from the Kinzers Formation of Pennsylvania, and Lieberman (1999) suggested that *Bolbolenellus hermani* occurred in both Vermont and California (but the Cordilleran material was described as *B. brevispinus* by Palmer [1998b]). Other putative circum-continental correlations have been based only on genus-level similarity (e.g., Fritz 1972, 1975; Palmer & Repina 1993).

Three of the newly documented olenelloids from Vermont are potentially conspecific with (or at least, extremely closely related to) forms from the southern Great Basin. First, *Bolbolenellus* cf. *brevispinus* from the Monkton Formation (Powerline section, ICS-10507) appears to be conspecific with *B. brevispinus* from the *Nephrolenellus multinodus* Zone of California and Nevada (Palmer 1998b; Webster 2011a). Second, *Olenellus* aff. *fowleri* from the Parker Formation (the PQL fauna) and the Monkton Formation (Powerline section, ICS-10508) is very similar to and possibly conspecific with *O. aff. fowleri* that occurs in the upper *Bolbolenellus euryparia* Zone of the southern Great Basin (Webster 2011a). Finally, *O. aff. transitans* from the PQL fauna is very similar to and possibly conspecific with *O. puertoblancoensis* (Lochman, 1952) from the *Bolbolenellus euryparia* Zone of the southern Great Basin (Webster 2011a, b).

Unfortunately, none of these three examples offer unambiguous species-level correlation because in each case either the Appalachian and/or the Cordilleran form is known from very few and/or poorly preserved specimens. The fact that all three Vermont taxa are left in open nomenclature reflects this uncertainty. However, new material of *Olenellus* aff. *fowleri* and *O. puertoblancoensis* has been collected from Nevada and is currently under study by MW; it is expected that these new data will resolve the ambiguity regarding whether or not the Cordilleran and Appalachian forms are conspecific. Pending completion of those studies, the six localities in the Parker Formation and Monkton formations studied herein are provisionally correlated with the *Bolbolenellus euryparia* Zone or overlying uppermost Dyeran *Nephrolenellus multinodus* Zone of the southern Great Basin.

This biostratigraphic correlation implies that the regression(s), of which the Monkton Formation is a sedimentary expression, must have been broadly contemporaneous with one or more of the four late Dyeran shallowing-up events that have been recognised in the southwestern United States, three of which occur within the *Bolbolenellus euryparia* and *Nephrolenellus multinodus* zones (Webster 2011a). It has also been suggested that the Monkton Formation is a local signature in Vermont of the Hawke Bay regression that was originally named for successions in western Newfoundland (Palmer & James 1979; Lavoie *et al.* 2003; Landing *et al.* 2006, 2009;

Landing 2007, 2012). Such temporal coincidence on a circum-continental scale suggests that the regression(s) were a eustatic rather than epeirogenically controlled phenomenon. This encourages further work to resolve more precisely which of the Cordilleran sequence boundaries corresponds to the Monkton Formation or surfaces therein, and how these in turn relate to events on a global scale (Landing *et al.* 2006).

MATERIAL AND METHODS

Material

All specimens mentioned herein are housed in the collections of the American Museum of Natural History, New York (AMNH), the Field Museum, Chicago (FMNH), the Institute for Cambrian Studies, Department of the Geophysical Sciences, University of Chicago (ICS), the Museum of Comparative Zoology, Harvard University (MCZ), the New York State Museum, Albany (NYSM), the former Princeton University museum (PUM; material subsequently transferred to the USNM and held there as a distinct collection), the Smithsonian Institution, United States National Museum of Natural History, Washington, D. C. (USNM), and the Yale Peabody Museum, Yale University (YPM). The new material collected as part of this study is housed in the FMNH and the ICS.

For several of the species discussed herein, neotypes have been designated by previous authors because the holotype has been lost, although plaster casts of the holotype exist. In such cases the neotype is valid despite the existence of plaster casts of the holotype because ICZN article 72.5.3 specifies that, in the case of fossils, an eligible name-bearing type specimen must be “a natural replacement, natural impression, natural mould, or natural cast of an animal or colony” (International Commission on Zoological Nomenclature 1999). A plaster cast is not naturally formed, and cannot serve as a type.

Species concept

Under the unified species concept, a species is defined as a segment of a separately evolving metapopulation lineage (de Queiroz 2007). Herein, as is typical for palaeontological studies, species are operationally delimited using the diagnosability criterion—a species is therefore recognised as the least inclusive aggregation of comparable individuals diagnosable by a unique combination of character states (Nixon & Wheeler 1990; Wheeler & Platnick 2000). Most olenelloid species are diagnosed on the basis of discrete or qualitative differences from other species (or at least differences in quantitative traits that are sufficiently large to be treated as qualitative differences). In some cases, however, species diagnosis is based on a statistically significant difference in a quantitative feature. As always, species delimitation is a hypothesis and is subject to rejection in the face of additional data. Taxonomic assignments that are based on limited currently available data, and are thus most likely to be subject to future revision, are explicitly highlighted herein.

Morphological terminology

The morphological terminology applied herein largely follows that of Palmer & Repina (1993) and Whittington & Kelly in Whittington *et al.* (1997), with modifications to olenelloid terminology proposed by Palmer (1998b), Webster (2007a, b, 2009b) and Webster & Bohach (2014). Following Webster (2007b, 2009b), genal spine advancement is measured by finding the point at which

the axial furrow is intersected by a transverse line drawn between the adaxial margins of the genal spine bases where they contact the posterior cephalic margin. The qualitative location of this point of intersection relative to the contact of the glabellar lobes and furrows with the axial furrow is expressed in the descriptions. Divergence of the ocular lobe from an exsagittal line is measured as the angle between an exsagittal line and a line from the posterior tip of the ocular lobe to the contact of the inner margin of the ocular lobe with the lateral margin of L3.

Ontogenetic development of the olenelloid cephalon has been divided into five distinct and successive phases (Webster *et al.* 2001; Webster 2007a, b, 2009b, 2015; Webster & Bohach 2014; see Webster 2007a for a discussion of how these phases relate to other subdivisions of trilobite ontogeny). This scheme of subdividing cephalic development offers a useful framework for describing and comparing olenelloid cephalic ontogeny. All specimens examined herein are in phase 5 of this framework and are considered morphologically mature. Some allometric growth continues through phase 5, and is described where appropriate.

Morphometric analyses

Many specimens studied herein are incompletely preserved. Standard geometric morphometric analyses of shape cannot accept missing data for any given landmark configuration, and are therefore frustrated in this particular case by cripplingly low sample size. Quantitative analyses of form are herein restricted to traditional morphometric variables (length and angular measures). Such variables can be studied individually or in pairs as well as in a multivariate analysis, and sample size therefore tends to be higher.

Traditional morphometric data were taken from digital images of specimens. Data were collected using the ImageJ software (<http://rsb.info.nih.gov/ij/index.html>). Values for some variables were estimated on incompletely preserved specimens, but only when those estimates were replicable within a small margin of error (typically < 0.05 mm on large cephalata). Values for variables relating to transverse measurements that span the sagittal line were obtained on some specimens by doubling a transverse measurement from the sagittal line to one end-point of the variable. Such estimates are designated as “approximate” values in the descriptions. Measurement error introduced through these approximations is likely to be negligible. Univariate and bivariate visualisation and analyses of traditional morphometric data were performed in the R software package (R Core Team 2013; <http://www.r-project.org/>).

SYSTEMATIC PALAEOLOGY

Order REDLICHIIA Richter 1932
Suborder OLENELLINA Walcott 1890b
Superfamily OLENELLOIDEA Walcott 1890b

Remarks. Generic and familial assignments for the species studied herein follow Lieberman (1998, 1999), because those works include the most recent published diagnoses of the relevant clades. Unfortunately, the phylogenetic analyses presented by Lieberman (1998, 1999) are compromised by numerous coding errors (below; see also Webster 2007a, 2009b; Webster & Bohach 2014) and by the failure to consider ontogenetic data (for the potential significance of this, see discussions by Webster & Bohach 2014 and Webster 2015). A new, comprehensive phylogenetic analysis and systematic revision of the Olenelloidea is

currently being conducted in order to address such problems (MW in preparation). Until such work is completed, current diagnoses (and thus membership) of olenelloid clades should be considered provisional.

Family OLENELLIDAE Walcott 1890b

Mesonacis Walcott 1885

Type species. *Olenus vermontana* Hall 1859a.

Mesonacis vermontanus (Hall 1859a) (Fig. 5)

1859a *Olenus vermontana*; Hall, p. 60, 61, fig. 2.

1859b *Olenus vermontana* Hall; Hall, p. 527, text-fig. on p. 527.

1860 *Barrandia Vermontana* (Hall); Hall, p. 117, text-fig. on p. 117.

1860b *Paradoxides Vermonti* (Hall); Emmons, p. 280, note A.

1861 *Barrandia Vermontana* (Hall); Hall (part), p. 370, reference to pl. 13, fig. 2 only [not reference to pl. 13, figs 4, 5 = *Olenellus transitans* or *O. brachycephalus*].

1861 *Paradoxides vermontana* (Hall); Marcou, p. 241, 245.

1861 *Paradoxides vermontana* (Hall); Barrande, p. 277, 278, pl. 5, fig. 8.

?1861 *Paradoxides vermontana* (Hall); Billings, p. 11.

1862a *Barrandia Vermontana* (Hall); Hall (part), pl. 13, fig. 2 only [not pl. 13, figs 4, 5 = *O. transitans* or *O. brachycephalus*].

1862b *Olenellus Vermontana* (Hall); Hall, p. 114.

?1862a *Paradoxides vermontana* (Hall); Billings, p. 950.

1862b *Paradoxides vermontana* (Hall); Billings, p. 100, 101?, 102, 104.

1863 *Paradoxides vermontana* (Hall); Billings in Logan *et al.*, p. 953.

?1865 *Olenellus Vermontana* (Hall); Billings, p. 11.

1871 *Paradoxides vermontiana* (Hall); Harkness & Hicks, p. 394, 398.

1877 *Olenellus vermontanus* (Hall); Linnarsson, p. 362.

1879 *Olenellus vermontana* (Hall); Brögger, p. 45.

1881 *Olenellus vermontanus* (Hall); Ford, p. 255, fig. 13.

1883 *Olenellus Vermontana* (Hall); Hague, p. 257.

1884 *Olenellus Vermontana* (Hall); Whitfield, p. 152, 153 [considered to be synonymous with *Olenellus thompsoni*].

1884 *Olenellus Vermontana* (Hall); Walcott, p. 34, 38.

1885 *Olenellus Vermontana* (Hall); Marcou, p. 217, 218, 224.

1885 *Mesonacis vermontana* (Hall); Walcott, p. 328–330, figs 1, 2.

1886 *Mesonacis vermontana* (Hall); Walcott, p. 15, 47, 158–162, pl. 24, figs 1, 1a, 1b.

1886 *Olenellus Vermontana* (Hall); Brögger, p. 183, 184.

1887 *Olenellus Vermontana* (Hall); Holm, p. 515, 516.

1888 *Olenellus Vermontana* (Hall); Marcou, p. 126.

1889 *Mesonacis vermontana* (Hall); Miller, p. 556, fig. 1031.

1889 *Mesonachis* [sic] *vermontana* (Hall); Lesley, p. 399–401, text-figs 1, 1a, 1b on p. 401.

1889 *Olenellus (Mesonacis) Vermontana* (Hall); Walcott, p. 377.

1890b *Olenellus (Mesonacis) vermontana* (Hall); Walcott, p. 637, pl. 87, figs 1, 1a, 1b.

1890a *Elliptocephalus (Schmidtia) vermontana* (Hall); Marcou, p. 363.

1892 *Olenellus (Mesonacis) vermontana* (Hall); Cole, p.

340, 341, fig. 2, p. 343.

1893 *Olenellus vermontana* (Hall); Vogdes, p. 327, 328.

1899 *Mesonacis vermontana* (Hall); Moberg, p. 314, 315, 318, pl. 13, fig. 4.

1910 *Mesonacis vermontana* (Hall); Walcott, p. 264–266, pl. 26, figs 1–3, pl. 44, fig. 2.

1910 *Mesonaces* [sic] *vermontana* (Hall); Grabau & Shimer, p. 264, fig. 1555f.

1912a *Mesonacis vermontana* (Hall); Walcott, p. 141?, 188, 247?, 251, 281?.

1916b *Mesonacis vermontana* (Hall); Walcott, pl. 45, fig. 2.

1917 *Mesonacis vermontana* (Hall); Walcott, p. 66, pl. 9, fig. 3.

1931 *Mesonacis vermontana* (Hall); Bell, p. 10, 11, 18, 20.

1936 *Mesonacis vermontana* (Hall); Grabau, p. 27, 29?, 123.

1937 *Mesonacis vermontana* (Hall); Schuchert, p. 1008, 1026, 1032, 1033, 1035.

1937 *Olenellus (Mesonacis) vermontana* (Hall); Raw, p. 579, 588.

1938 *Olenellus vermontanus* (Hall); Resser & Howell, p. 220, 221, text-fig. 1.2, pl. 4, figs 15, 16.

1938 *Olenellus georgiensis*; Resser & Howell (part), p. 220, pl. 5, fig. 7 only [not pl. 5, fig. 6 = *Olenellus* aff. *fowleri*].

1944 *Olenellus vermontanus* (Hall); Shimer & Shrock, p. 613, pl. 253, fig. 1.

1948 *Olenellus vermontanus* (Hall); Kindle & Tasch (part), p. 134, 136, pl. 1, figs 5, 6?.

1949 *Olenellus vermontanus* (Hall); Tasch, table 1.

1952 *Olenellus vermontanus* (Hall); Best, p. 20.

1952 *Olenellus vermontanus* (Hall); Hupé, p. 122.

1952 *Olenellus georgiensis* Resser & Howell; Hupé, p. 122.

1953 *Olenellus vermontanus* (Hall); Hupé, p. 128, fig. 51 (2).

1953 *Olenellus georgiensis* Resser & Howell; Hupé, p. 128.

1953 *Olenellus vermontanus* (Hall); Raw, p. 96 (reported as *Olenellus vermontana*), fig. 3g.

1954 *Olenellus vermontanus* (Hall); Shaw, p. 1040, 1041.

1955 *Olenellus vermontanus* (Hall); Shaw (part), p. 793, 794 only [not pl. 75, fig. 10 = olenelloid sp. indet.].

1956 *Olenellus vermontanus* (Hall); Lochman, p. 1354.

1957 *Olenellus vermontanus* (Hall); Raw, p. 149, 150, 178 [in places reported as *Olenellus vermontana*], text-fig. 1g.

1957 *Olenellus georgiensis* Resser & Howell; Raw, p. 149, 150.

1957b *Olenellus vermontanus* (Hall); Shaw, p. 814.

1959 *Olenellus vermontanus* (Hall); Harrington in Harrington *et al.*, fig. 28a.

1960 *Olenellus vermontanus* (Hall); Kielan, p. 87.

1989 *Olenellus vermontanus* (Hall); Whittington, p. 120, 121, 131, 132, figs 14, 16, 18.

1993 *Olenellus (Mesonacis) vermontanus* (Hall); Palmer & Repina, p. 22, fig. 3.2.

1996 *Olenellus vermontanus* (Hall); Geyer, p. 158.

1997 *Olenellus (Mesonacis) vermontanus* (Hall); Palmer & Repina in Whittington *et al.*, p. 408, fig. 255.2.

1998 *Mesonacis vermontanus* (Hall); Lieberman, p. 66, 67, table 1, fig. 2 [cladogram].

1999 *Mesonacis vermontanus* (Hall); Lieberman, p. 3 [reported as *Mesonacis vermontana*], 28, 38, 41, 42, table 4, fig. 7 [cladogram].

1999 *Mesonacis vermontanus* (Hall); Smith & Lieberman, table 1.

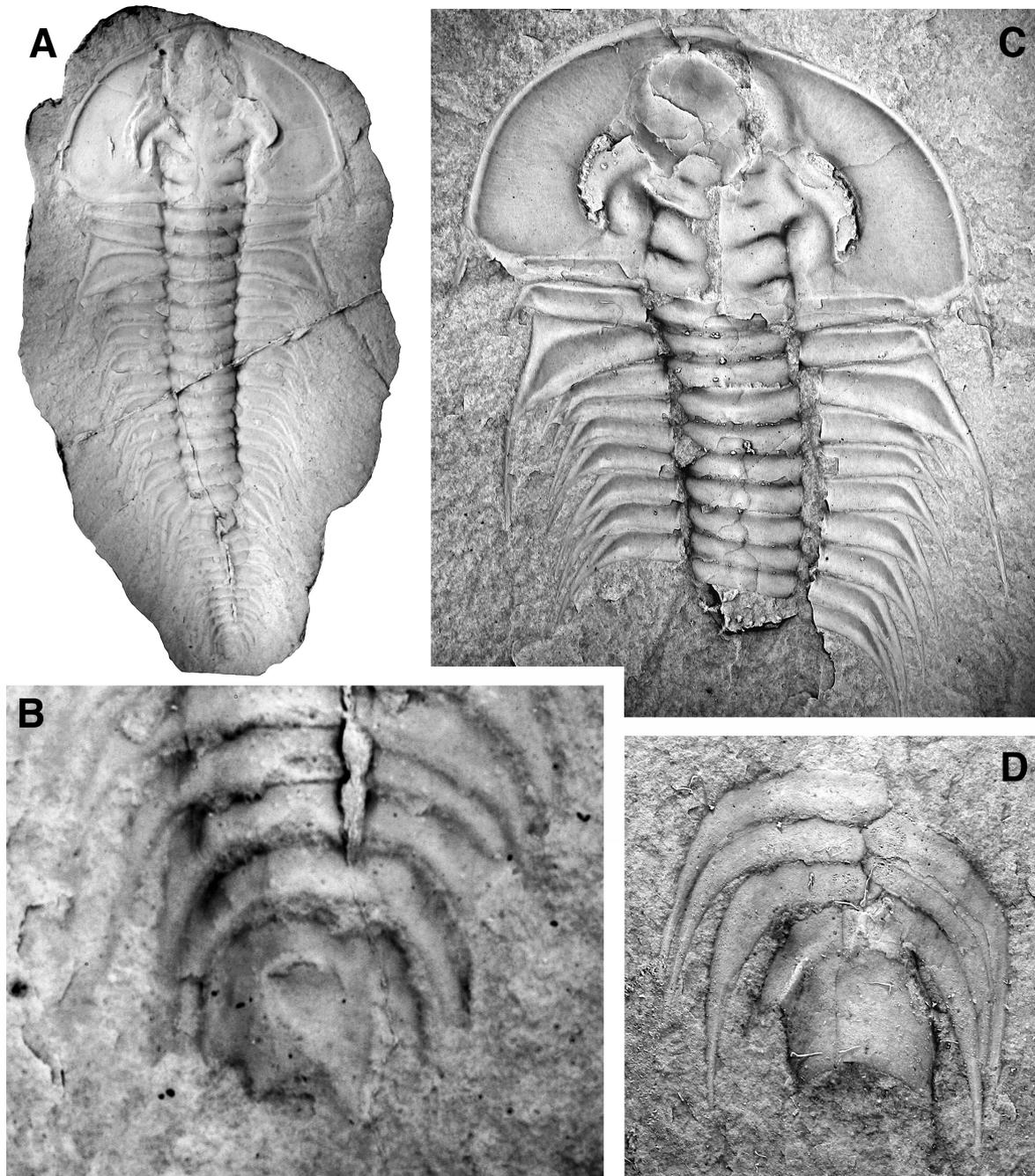


Figure 5. *Mesonacis vermontanus* from the Parker Formation, Parker quarry, Franklin County, Vermont. **A, B**, latex peel of external mould, USNM 15399a (neotype). **A**, complete dorsal exoskeleton, x1. **B**, enlargement of posterior portion of opisthothorax and pygidium, x7. **C, D**, disarticulated but almost complete dorsal exoskeleton, latex peel of external mould, FMNH UC21291. **C**, cephalon plus portion of prothorax, x2. **D**, portion of opisthothorax plus pygidium, x7. All in dorsal view.

2001 *Mesonacis vermontanus* (Hall); Lieberman, p. 101.

2002 *Mesonacis vermontanus* (Hall); Lieberman, fig. 2 [cladogram].

2003 *Mesonacis vermontanus* (Hall); Lieberman, table 1.

Holotype and neotype. The holotype is AMNH 230 (Appendix 2). Despite several searches, this specimen appears to be lost (see Resser & Howell 1938, p. 217; Whittington 1989, p. 120; Lieberman 1999, p. 41). Plaster casts of the holotype are in the USNM (USNM 62475; see Resser & Howell 1938, p. 220, 221, pl. 4, fig. 15) and in the Walker Museum collection (FMNH UC15941; formerly held at the University of Chicago, now at the

Field Museum). For an historical account of these casts see Resser & Howell (1938, p. 220). Lieberman (1999, p. 41) designated USNM 15399a as the neotype (Fig. 5A, B).

Other material. See Appendix 2 for material examined from the Parker Formation. Lieberman (1998, p. 67; 1999, p. 41) assigned MCZ 2434 and (tentatively) MCZ 108662 to *M. vermontanus*. However, both these identifications are questionable. The former specimen is too poorly preserved for definitive species-level identification, while the latter specimen preserves only the glabella, an interocular area, and an ocular lobe. The posterior tip of the ocular lobe of this specimen is located transversely opposite the

lateral margin of LO, and is markedly longer than the ocular lobe of any other specimen of the species (tips are invariably located opposite the lateral margins of L1). In the length of the ocular lobe and in the condition of the glabellar furrows this specimen more closely resembles *O. transitans*. Assignment of MCZ 108662 to *M. vermontanus* is therefore dubious, and the specimen is treated herein as a fragment of an indeterminate olenelloid.

Kindle & Tasch (1948) reported *M. vermontanus* from the Monkton Formation. Shaw (1962, p. 332) considered these specimens to represent *O. brachycephalus*, but at least one of the figured specimens appears to have been correctly identified (Kindle & Tasch 1948, pl. 1, fig. 5).

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25 and the effectively equivalent USNM Locality 319m, within the Parker Formation. A supposed occurrence in the lower part of the Kelly quarry cannot be confirmed (see above). Locality M-WC-1, Chittenden County: middle Monkton Formation (Kindle & Tasch 1948).

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin oriented more or less transversely, distal portion flexed anteriorly by approximately 40° relative to proximal portion at rounded adgenal angle located approximately 70% of distance from axial furrow to base of genal spine. Greatest observed cephalic length approximately 30 mm (sag.; Fig. 5A). Genal spine slender, base transversely opposite anterior portion of lateral margins of LO (Fig. 5C) or SO (Fig. 5A); length approximately one-third cephalic length (sag.). Intergenial spine reduced to tiny spine or node on posterior cephalic border between adgenal angle and base of genal spine. Cephalic border flattened, well defined around entire cephalon by distinct border furrow; width of anterior border opposite junction of ocular lobes with LA approximately one-third length (exsag.) of LO. Glabella weakly constricted at S1; approximately 93% of cephalic length (sag.), preglabellar field very short (sagittal length approximately equal to or less than that of anterior cephalic border; Fig. 5C; also USNM 90707) to absent (Fig. 5A), probably decreases in length during ontogeny. Maximum width of LA approximately 125% basal glabellar width (tr.). Posterior convexity of posterior margin of glabella difficult to determine due to taphonomic fracturing and incomplete preservation. SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subquadrate (Fig. 5A) to subtrapezoidal, slightly narrows anteriorly (Fig. 5C), length (exsag.) approximately 13% glabellar length (sag.). S1 deepest abaxially, approximately parallel to SO. L1 subtrapezoidal, slightly narrows anteriorly; length (exsag.) approximately 14% glabellar length (sag.). S2 and S3 slightly shallower than SO and S1. S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, abaxial end slightly anterior to adaxial end. L2 and L3 confluent distally, widen (tr.) anteriorly to point of contact with ocular lobes. S3 deepest midway between sagittal line and axial furrow, isolated from axial furrow, oriented anterolaterally away from axis to point of contact with ocular lobes. Axial furrow shallow at lateral margins of L3. LA slightly wider (tr.) than long (sag.), approximately 45–50% glabellar length (sag.), separated from extraocular area by a sharp break in slope, weakly convex (Kindle & Tasch 1948, pl. 1, fig. 5); widest point at intersection with anterior margin of ocular lobes. Weak

parafrontal band seems to be present around lateral margin of LA immediately anterior to intersection with ocular lobe, fades anteriorly (Fig. 5C, right side; it is possible that this is a taphonomic artefact). Tiny axial node on LO. Ocular lobes diverge from exsagittal line at approximately 20°, crescentic, flat-topped, posterior tip transversely opposite posterior half of lateral margin of L1; very shallow ocular furrow on anterior portion of ocular lobe, inner band slightly wider (tr.) than outer band (Fig. 5C, right side). Interocular area gently arched in transverse section, slightly wider (tr.) than ocular lobes and approximately 40–45% width (tr.) of extraocular area opposite S1. Weak posterior ocular line and extraocular genal caeca present. Bertillon markings on LA and on dorsal surface of lateral and posterolateral cephalic border and base of genal spines. Rostral plate unknown (although an impression of a fragment of this sclerite may be preserved on the anterior cephalon on USNM 90707). Impression of hypostome preserved beneath LA on FMNH UC21291 (Fig. 5C), USNM 90707 and USNM 62475, but of insufficient quality to describe.

Prothorax of 14 segments; axis marginally wider (tr.) than inner pleural region on T1, gently tapers posteriorly; axial furrow on each segment shallowest at ring midlength (exsag.). Axial node or spinelet developed on T3, axial node possibly present on T1 and T2, axial spinelet possibly present on T4 and T5; axial spinelet present on T14, axial structures tiny or absent on T6–T13 (interpretation hindered by compaction-related fractures). Inner pleural regions of T1 and T2 transverse, very slightly taper distally, with straight margins. T3 hyperpleural; pleural spine macrospinous with tip located transversely opposite axial ring of T9 or T10 (Fig. 5C; perhaps of T7 on neotype [Fig. 5A]). Inner pleural region of T4 and to lesser extent of T5 tapers distally to accommodate lateral expansion (exsag.) of T3. Inner pleural regions of T6–T8 transverse, parallel-sided, with straight margins. Inner pleural regions of T9–T14 increasingly divergent, parallel-sided, margins increasingly curved on more posterior segments. Pleural spine of T1, T2 and T4 sentate, very slender, divergent; those of T5–T14 falcate, progressively increasing in length posteriorly on the prothorax, all divergent, become subpendent on posterior segments. Pleural furrows wide (exsag.), occupying much of inner pleural region; steeper anteriorly; extending onto pleural spines of T3–T14, possibly also T2. Bertillon markings on pleural spine of T2 to at least T10, possibly weakly developed on abaxial portion of axis of at least T7 and T10.

Opisththorax of 11 segments (Fig. 5A, B). Slender axial spine on T15 almost as long as entire opisththorax; no axial structures on T16–T25. Axis defined by break in slope; axial furrow not incised. Inner pleural region of T15 approximately one-third width (tr.) of axial ring, strongly tapered, weakly divergent, margins curved; pleural spine slender, sentate. Inner pleural regions of T16–T20 transverse, weakly tapered to parallel-sided, margins straight; pleural spines slender, falcate, divergent, length of one to two axial rings, longer on more posterior segments. Inner pleural regions of T21–T25 increasingly divergent, parallel-sided, margins increasingly curved; pleural spines falcate, increasingly longer and divergent to subpendent on more posterior segments. Pleural furrow shallow on all opisththoracic segments, extremely so on more posterior segments, extends close to base of or onto pleural spines.

Pygidium consists of an opisththoracic-like segment fused to anterior margin of a subtrapezoidal plate-like portion

(Fig. 5B, D). Axis of anteriormost segment poorly defined by break in slope; pleura evenly tapered, subpendent, hugs anterolateral margin of posterior plate and extends into short, subpendent spine; inner pleural region not delineated from spine; pleural furrow extremely shallow or absent. Plate-like portion of pygidium subtrapezoidal, slightly narrows (tr.) posteriorly; weakly convex (tr.). Axis very weakly defined by break in slope, extends approximately three-fifths length (sag.) of plate-like portion, comprising one segment plus semicircular terminal piece defined by extremely shallow ring furrow. Pleural field of plate-like portion slopes down to pygidial margin, pygidial border not defined; furrow separates anterolateral margin of plate-like portion from pleura of anteriormost pygidial segment. Lateral margins of plate-like portion slightly convergent posteriorly; projecting into short marginal spines at posterolateral corners; posterior pygidial margin between spines concave.

Remarks. The neotype of *Mesonacis vermontanus* has been illustrated many times (Fig. 5A, B; Appendix 2), but the species is otherwise known from very few specimens (discussed above). A previously undocumented specimen (FMNH UC21291; Fig. 5C, D) preserves many features (including the pygidium; Fig. 5D) in finer detail than the neotype. Despite the detail of its preservation, FMNH UC21291 is unfortunately disarticulated and incomplete: T1–T10 remain articulated with the cephalon (Fig. 5C), while the posterior of the trunk (comprising the posterior three freely articulating segments of the opisthothorax plus the pygidium; Fig. 5D) is displaced slightly posteriorly and laterally. The posterior of the prothorax and anterior of the opisthothorax are missing. The two dissociated parts are considered to represent the same individual based on their close proximity (separation of approximately 20 mm), appropriate relative sizes and morphology (by comparison to the neotype; Fig. 5A).

Mesonacis vermontanus has been variably interpreted as having 25 or 26 thoracic segments (contrast Walcott 1910, pl. 26, figs 1, 2 and Whittington 1989, fig. 14 [both show 25 segments] to Walcott 1885, figs 1, 2 [with 26 segments]). The newly studied specimen FMNH UC21291 shows how this confusion may have arisen, and supports the interpretation offered by Whittington (1989). On both USNM 15399a (Fig. 5B) and FMNH UC21291 (Fig. 5D) an opisthothoracic-like trunk segment is fused to the anterior margin of a subtrapezoidal posterior plate-like structure and is separated from it by a furrow. On USNM 15399a this fused segment is clearly T26 (the identity of this segment is unknown on FMNH UC21291 due to disarticulation and missing segments). Based on the limited material available, it is unknown whether this fused state represents the final (holaspid) condition or whether this segment was in the process of being released into the opisthothorax. The posterior trunk therefore consists of an opisthothorax of at least 11 segments (T15–T25) followed by a pygidium comprising T26 fused to a posterior plate-like portion (perhaps representing the pygidium proper) that bore one axial ring plus a terminal piece. Walcott's reconstructions (1885, figs 1, 2; 1910, pl. 26, figs 1, 2) also show a median spine along the posterior pygidial margin, but FMNH UC21291 confirms Whittington's (1989, p. 121) suspicion that this is erroneous (Fig. 5D).

Olenellus georgiensis was named by Resser & Howell (1938, p. 220, pl. 5, figs 6, 7) based on nine specimens that

had formerly been assigned to *Mesonacis vermontanus*. All known specimens of *O. georgiensis* were from USNM locality 25, and all have experienced tectonic deformation. *Olenellus georgiensis* was stated to differ from *M. vermontanus* in being wider and having narrower opisthothoracic segments with long pleural spines; and to differ from *O. thompsoni* in having stronger intergenal spines. Shaw (1955, p. 794) reassigned both specimens figured by Resser & Howell (1938) to *M. vermontanus*. Lieberman (1999) considered only the holotype of *O. georgiensis* (Resser & Howell 1938, pl. 5, fig. 7) to represent *M. vermontanus*; he reassigned the second specimen (Resser & Howell 1938, pl. 5, fig. 6; Fig. 13A herein) to *O. thompsoni*. The present study supports Shaw (1955) and Lieberman (1999) in terms of the reassignment of the former holotype of *O. georgiensis* to *M. vermontanus* (thus rendering *O. georgiensis* a junior subjective synonym of *M. vermontanus*), but differs from all previous authors in recognising the second specimen of *O. georgiensis* (Resser & Howell 1938, pl. 5, fig. 6; Fig. 13A) as a distinct taxon herein named *O. aff. fowleri*.

Mesonacis vermontanus was included in a cladistic analysis of olenelloid trilobites by Lieberman (1998). That analysis placed *M. vermontanus* as a sister species to *Mesolenellus hyperborea* (Poulsen 1974); this clade was in turn sister to a clade of *Olenellus* species. Such a close relationship between *Mesonacis* Walcott 1885, *Mesolenellus* Palmer & Repina 1993 and *Olenellus* Hall in Billings 1861 is congruent with the taxonomic classification of the Olenelloidea Walcott 1890b by Palmer & Repina (1993; Palmer & Repina in Whittington *et al.* 1997) in which *Mesonacis* and *Mesolenellus* were treated as subgenera of *Olenellus*. However, this report has prompted the revision of the state assignment for several characters of *M. vermontanus* in Lieberman's (1998) analysis. These revisions (and those detailed below for other species) are incorporated into a new phylogenetic analysis of olenelloid trilobites (MW in preparation), but presentation of that analysis lies beyond the scope of the current paper. In the following reevaluation of character coding, the designations "earlier" or "originally" refer to Lieberman's (1998) analysis.

A preglabellar field (character 5; also character 3 of Lieberman 1999, Mesonacinae analysis) is absent on the neotype (state 1, as originally coded; Fig. 5A), but is present on other specimens (state 0; Fig. 5C, also USNM 90707). Character 5 should therefore be treated as polymorphic (states 0 and 1). The presence or absence of a parafrontal band (character 7; originally coded as absent [state 1]) cannot be reliably determined owing to compaction-related deformation of all specimens, and should accordingly be coded as state unknown. A weak parafrontal band seems to be present, at least around the posterior portion of the lateral margin of LA, on some specimens (Fig. 5C, right side). The lateral margins of LA (character 11; see also character 16 in Lieberman 1999, Mesonacinae analysis) are consistently slightly distal to the lateral margins of LO (state 1; Fig. 5A, C; this had originally been coded as directly anterior to the lateral margins of LO [state 2]). A prominent eye socle separates the ocular lobe from the extraocular area on all specimens (e.g., Fig. 5C, right side), and the ocular lobe is therefore consistently separated from the extraocular area by a prominent shelf and/or furrow (character 16, state 0; this had originally been coded as smoothly merging into the extraocular area [state 1]). The transverse profile of the

ocular lobes (character 21) was originally coded as convex (state 0) but appears to be rather flattened (state 1; Fig. 5C). The surface of the interocular area (character 22) is gently arched (state 2; Fig. 5C); this had originally been coded as a flattened shelf (state 1). Whether S3 crosses the sagittal line (character 28) cannot be reliably determined owing to compaction-related deformation, and this character should therefore be treated as state unknown (it had originally been coded as not conjoined medially [state 1]). The posterior convexity of the posterior margin of the glabella is difficult to determine due to taphonomic fracturing and incomplete preservation on all material, and character 41 should therefore be treated as state unknown (this had originally been coded as roughly transverse [state 0]). The extraocular area (character 44) appears to be gently convex (state 2) on non-compacted material (Kindle & Tasch 1948, pl. 1, fig. 5); this had originally been coded as flattened (state 0). Genal caeca are developed on the extraocular area (character 45, state 0; Fig. 5C); they had originally been coded as absent (state 1). A genal ridge was not visible on any specimen examined herein (character 47, state 1; this had originally been coded as being prominently developed [state 0]). An intergenal ridge was not visible on any specimen examined herein (character 48, state 1; this had originally been coded as being visible as a trace [state 0]). The transverse width of the extraocular area relative to that of the glabella at L1 (character 49) is 78% on the left side of the neotype (right side inadequately preserved) and 88% and 89% on the left and right sides of FMNH UC21291, corresponding to state 0; this had originally been coded as state 1 (40% to 50%). The base of the genal spines lies transversely opposite the lateral margins of LO (character 52, state 0; Fig. 5C) or SO (no state defined; Fig. 5A); this had originally been coded as opposite the distal margin of L1 (state 1). The intergenal angle is developed posterior to a point midway between the ocular lobes and genal spine (character 53, state 2; as coded by Lieberman 1999, Mesonacinae analysis, character 5); Lieberman (1998) coded this as adjacent to or directly behind the genal spine (state 0). The intergenal spine (character 54) is a tiny spine (Fig. 5C; state 2; as originally coded) or is reduced to a tiny posteriorly directed node (state 4; Fig. 5A), and character 54 should therefore be treated as polymorphic (states 0, 2). The posterior tip of the pleural spine of T3 (character 60; see also character 14 of Lieberman 1999, Mesonacinae analysis) is transversely opposite the axial ring of T9 or T10 (Fig. 5C; state 1) or T7 (Fig. 5A; state 3, as originally coded); character 60 should therefore be treated as polymorphic (states 1, 3). The original flexure of the tips of the thoracic pleurae relative to the more proximal portion of the pleurae (character 71) is difficult to ascertain from the compacted material available, and this character should be conservatively coded as state unknown (earlier coded as 0 [roughly in same dorsoventral plane]). Quantification of the length (sag.) to width (tr.) ratio of the pygidium (character 78) depends on whether the entire pygidium (i.e., opisthothoracic-like anteriormost segment plus the posterior plate-like portion) or just the posterior plate-like portion is interpreted as the pygidium (see above)—the posterior plate-like portion is slightly wider than long, whereas the entire pygidium is more or less equidimensional (state 1). Lieberman (1998) originally coded this character as state 0 (length 1.5 times width).

Olenellus Hall in Billings 1861

Type species. *Olenus thompsoni* Hall 1859a.

Olenellus thompsoni (Hall 1859a) (Figs 6, 7)

- 1859a *Olenus thompsoni*; Hall, p. 59, fig. 1.
 1859b *Olenus thompsoni* Hall; Hall, p. 525, 526, text-fig. on p. 526.
 1860 *Barrandia Thompsoni* (Hall); Hall, p. 115, 116, text-fig. on p. 116.
 1860b *Paradoxides Thompsoni* (Hall); Emmons, p. 280, note A.
 1861 *Barrandia Thompsoni* (Hall); Hall, p. 369, 370.
 1861 *Paradoxides (Olenellus) Thompsoni* (Hall); Marcou, p. 241, 245.
 1861 *Paradoxides Thompsoni* (Hall); Barrande, p. 276, pl. 5, fig. 6.
 ?1861 *Paradoxides Thompsoni* (Hall); Billings, p. 11.
 1862a *Barrandia Thompsoni* (Hall); Hall, pl. 13, fig. 1.
 1862b *Olenellus thompsoni* (Hall); Hall, p. 114.
 ?1862a *Paradoxides Thompsoni* (Hall); Billings, p. 950.
 1862b *Paradoxides Thompsoni* (Hall); Billings, p. 100, 101?, 102, 104.
 1863 *Paradoxides Thompsoni* (Hall); Billings in Logan *et al.*, p. 953.
 ?1865 *Olenellus thompsoni* (Hall); Billings, p. 11.
 1871 *Paradoxides Thompsoni* (Hall); Harkness & Hicks, p. 394, 398.
 1875 *Paradoxides Thompsoni* (Hall); Brögger, p. 574.
 1877 *Olenellus thompsoni* (Hall); Linnarsson, p. 362.
 1879 *Olenellus thompsoni* (Hall); Brögger, p. 45.
 1881 *Olenellus thompsoni* (Hall); Ford, p. 251, fig. 12.
 1883 *Olenellus thompsoni* (Hall); Hague, p. 257.
 not 1884 *Olenellus thompsoni* (Hall); Whitfield, p. 151–153, pl. 15, figs 1–4 [pl. 15, figs 1, 2 = *Olenellus transitans*; pl. 15, fig. 3 = *Olenellus transitans*?; pl. 15, fig. 4 = *Olenellus* sp. indet.].
 1884 *Olenellus thompsoni* (Hall); Walcott, p. 38.
 1885 *Olenellus thompsoni* (Hall); Marcou, p. 217, 218, 224, 228?.
 1885 *Olenellus thompsoni* (Hall); Walcott, p. 330.
 1886 *Olenellus thompsoni* (Hall); Walcott (part), p. 15, 18?, 19?, 26?, 29?, 32?, 38?, 47, 163, 164, 167, 168, pl. 17, fig. 2 only [not pl. 17, fig. 1 = *Olenellus crassimarginatus*; not pl. 17, fig. 4 = olenelloid sp. indet.; not pl. 17, fig. 9 = *Olenellus* sp. indet.; not pl. 22 or pl. 23 = *Olenellus agellus*].
 1886 *Olenellus thompsoni* (Hall); Brögger, p. 182, 183, 184.
 1887 *Olenellus thompsoni* (Hall); Holm, p. 514.
 1888 *Olenellus thompsoni* (Hall); Marcou, p. 108, 112?, 115?, 117, 126?, 127.
 1888 *Olenellus thompsoni* (Hall); Walcott, p. 234?, 236?, 317?.
 1889 *Olenellus thompsoni* (Hall); Marcou, p. 60?, 64?, 68?.
 1889 *Elliptocephala thompsoni* (Hall); Miller, p. 546, fig. 1003.
 1889 *Olenellus thompsoni* (Hall); Lesley (part), p. 491, 492, text-fig. on p. 491 labelled pl. 17, fig. 2 only [not specimen labelled pl. 22 = *Olenellus agellus*; not specimen labelled pl. 17, fig. 9 = *Olenellus* sp. indet.].
 1889 *Olenellus thompsoni* (Hall); Walcott, p. 377.
 1890a *Elliptocephalus (Olenellus) thompsoni* (Hall); Marcou, p. 363.
 1890b *Elliptocephalus (Olenellus) thompsoni* (Hall); Marcou, p. 91, 92?, 93?.
 1890b *Olenellus (Elliptocephalus) thompsoni* (Hall); Marcou, p. 89.

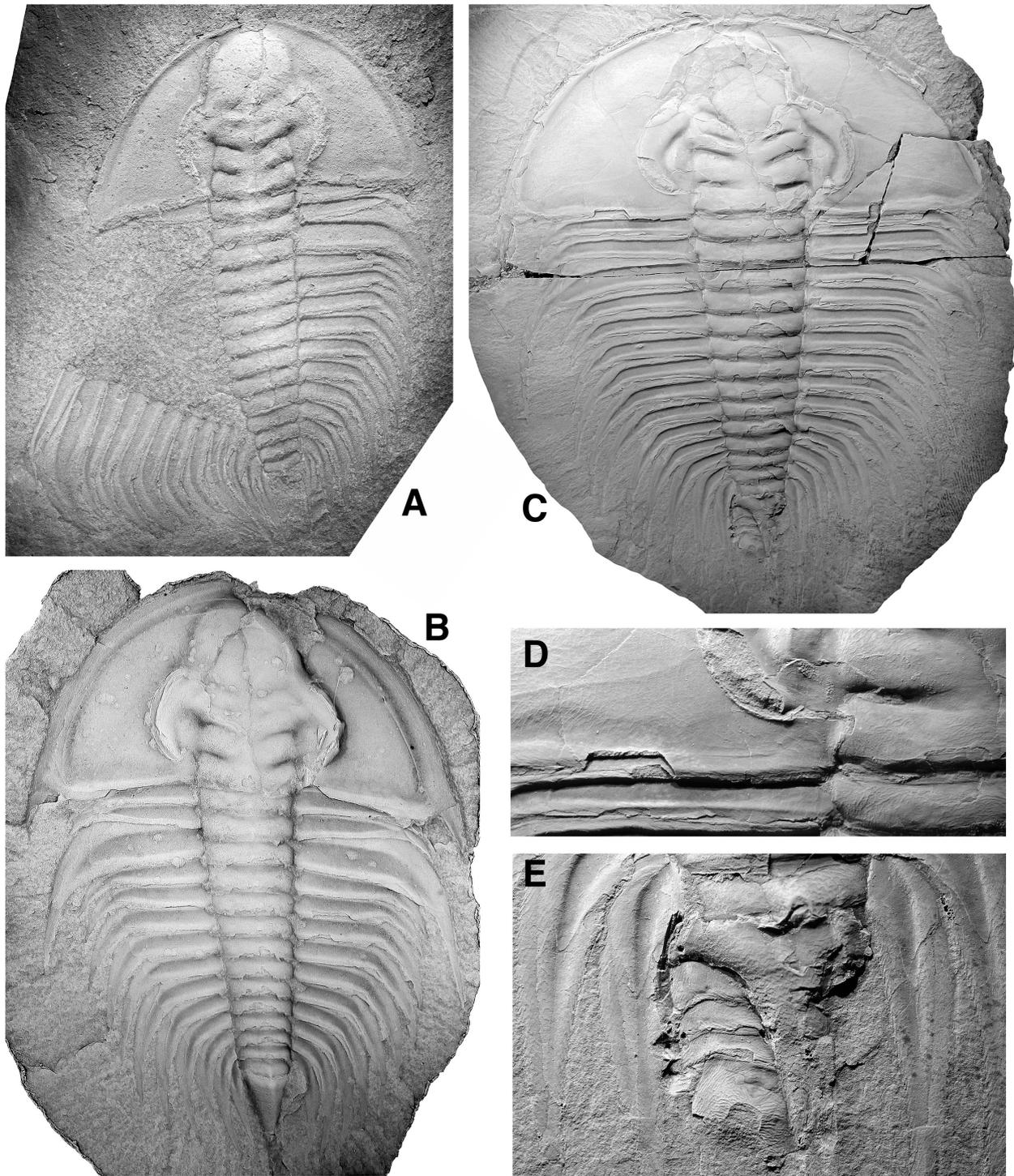


Figure 6. *Olenellus thompsoni* from the Parker Formation, Parker quarry, Franklin County, Vermont. **A**, internal mould, USNM 15418c (neotype), x1. **B**, latex peel of external mould, USNM 15418a, x2. **C–E**, complete dorsal exoskeleton, internal mould, USNM 56808a. **C**, entire specimen, x0.8. **D**, details of portion of cephalon and first thoracic segment, x2. **E**, details of opisthothorax and pygidium, x3. All in dorsal view.

1890b *Olenellus thompsoni* (Hall); Marcou, p. 88?, 100.

1890a *Olenellus thompsoni* (Hall); Walcott, p. 43.

1890b *Olenellus thompsoni* (Hall); Walcott (part), p. 635, pl. 83, fig. 1a only [not pl. 82, fig. 1 = *Olenellus agellus*; not pl. 82, fig. 1a = *Olenellus* sp. indet.; not pl. 83, fig. 1 = *Olenellus agellus*; not pl. 83, fig. 1b = *Olenellus crassimarginatus*].

1892 *Olenellus thompsoni* (Hall); Cole, p. 340, 341, fig. 1.

?1892 *Olenellus thompsoni* (Hall); Walcott, p. 52, 53.

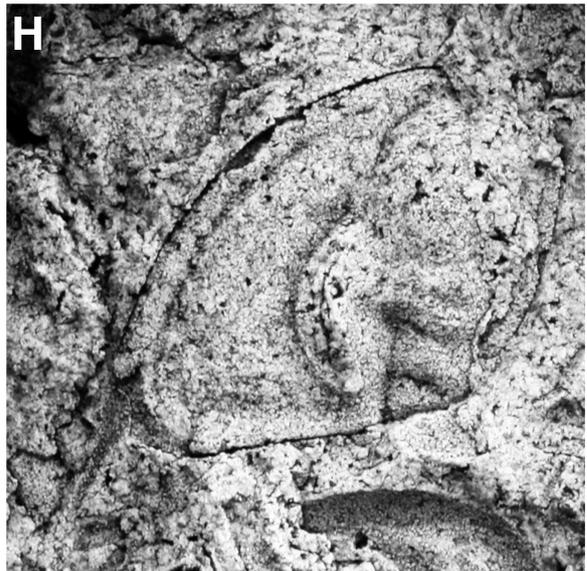
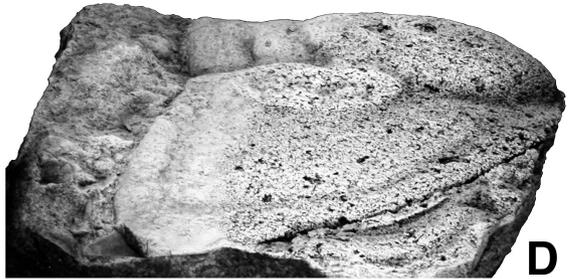
1893 *Olenellus thompsoni* (Hall); Vogdes, p. 327.

?1896 *Olenellus thompsoni* (Hall); Walcott, p. 16 footnote. not 1897 *Olenellus thompsoni* (Hall); Frech, pl. 1a, fig. 7 [= *Olenellus agellus*].

1899 *Olenellus thompsoni* (Hall); Moberg, p. 314, 317, pl. 13, fig. 2.

not 1901 *Olenellus thompsoni* (Hall); Lindström, p. 12 [=

- Olenellus agellus*].
 not 1903 *Olenellus thompsoni* (Hall); Woodward, p. 297, fig. 1 [= *Corynexochine* sp. indet.].
 1906 *Olenellus thompsoni* (Hall); Clark & Mathews, pl. 16, fig. 16.
 1909 *Olenellus thompsoni* (Hall); Walcott, p. 198.
 1910 *Paedeumias transitans* Walcott (part), p. 305, pl. 24, fig. 12, pl. 33, fig. 1, pl. 44, figs 7, 8 only.
 1910 *Olenellus thompsoni* (Hall); Walcott (part), p. 336–340, pl. 34, fig. 9 only [not pl. 35, fig. 1 = *Olenellus agellus*; not pl. 35, figs 2, 3 = species indeterminate; not pl. 35, fig. 4 = *Olenellus* sp. indet.; not pl. 35, figs 5, 5a, 6 = *Arcuolenellus rudis* (Resser 1938); not pl. 35, figs 7, 7a = hypostome questionably assigned to *A. rudis*].
 not 1910 *Olenellus thompsoni* (Hall); Grabau & Shimer, p. 263, figs 1555a, b [a = *Olenellus agellus*; b = *Olenellus* sp. indet.].
 1912a *Olenellus thompsoni* (Hall); Walcott (part), p. 147?, 188, 200?, 201?, 211?, 250, 251, 266?.
 ?not 1912b *Olenellus thompsoni* (Hall); Walcott, p. 240.
 1916 *Olenellus thompsoni* (Hall); Matthew, p. 54.
 not 1919 *Olenellus thompsoni* (Hall); Bassler, p. 339, pl. 24 [= *Olenellus agellus*].
 not 1926 *Olenellus thompsoni* (Hall); Butts, p. 68, pl. 5, figs 20–22 [= *Olenellus buttsi* Resser 1938].
 not 1927 *Olenellus thompsoni* (Hall); Raw, p. 133, 137, 138, 139, 143, figs 22–25 [= *Olenellus roddyi* Resser & Howell 1938].
 not 1928 *Olenellus thompsoni* (Hall); Raymond, p. 169 [= *Olenellus roddyi*].
 1931 *Olenellus thompsoni* (Hall); Bell (part), p. 2, 4, 20 only [not figs 1, 2 = *Olenellus* sp.; not fig. 3 = *Olenellus roddyi*?; not fig. 4 = *Olenellus transitans*].
 1933 *Olenellus thompsoni* (Hall); Resser, p. 747, table 1?.
 1936 *Olenellus thompsoni* (Hall); Grabau, p. 12?, 14?, 20?, 26?, 27, 60?, table 1, table 2.
 1937 *Olenellus thompsoni* (Hall); Raw (part), p. 579, 588 only [not p. 592, referring to Bell 1931, figs 1–3].
 1937 *Olenellus thompsoni* (Hall); Schuchert, p. 1008, 1011, 1024?, 1026, 1027, 1030?, 1032?, 1033?, 1034?, 1035?, 1036?.
 1938 *Olenellus thompsoni* (Hall); Resser & Howell, p. 219, 220, text-fig. 1.1, pl. 3, figs 17–19.
 1940 *Olenellus thompsoni* (Hall); French, p. 325, pl. 1, fig. 16.
 1944 *Olenellus thompsoni* (Hall); Shimer & Shrock, p. 613, pl. 253, fig. 4.
 ?1948 *Olenellus thompsoni* (Hall); Kindle & Tasch, p. 134, 135, 136 [not pl. 1, fig. 4 = olenelloid sp. indet.; not pl. 2, fig 4 = olenelloid sp. indet.].
 ?1949 *Olenellus thompsoni* (Hall); Tasch, table 1.
 1952 *Olenellus thompsoni* (Hall); Best, p. 20.
 1952 *Olenellus thompsoni* (Hall); Hupé (part), p. 122, text-fig. 69.2 only [not p. 276, referring to Walcott 1910, pl. 35, figs 3, 7].
 1953 *Olenellus thompsoni* (Hall); Hupé, p. 128, fig. 77.2.
 1953 *Olenellus thompsoni* (Hall); Raw, p. 96 [referring to Walcott 1910, pl. 33, fig. 1].
 1954 *Olenellus thompsoni* (Hall); Shaw, p. 1040, 1041, 1042?, 1045.
 1955 *Olenellus thompsoni* (Hall); Shaw (part), p. 775, 792, 793 [not references that synonymise *Olenellus crassimarginatus* and *Olenellus agellus*].
 ?1955 *Olenellus thompsoni* (Hall); Bloomer & Werner, p. 597.
 ?1956 *Olenellus thompsoni* (Hall); Fisher, p. 339.
 not 1956 *Olenellus thompsoni* (Hall); Harrington, text-fig. 1a [= *Olenellus agellus*?].
 1956 *Olenellus thompsoni* (Hall); Lochman, p. 1377, table 3 (p. 1354).
 1957b *Olenellus thompsoni* (Hall); Shaw, p. 814.
 1957 *Olenellus thompsoni* (Hall); Raw (part), p. 149, 172 only [not text-fig. 5b = *Olenellus agellus*; a paper model based on Walcott 1910, pl. 35].
 ?1958 *Olenellus thompsoni* (Hall); Lochman-Balk & Wilson, p. 320.
 not 1959 *Olenellus thompsoni* (Hall); Harrington in Harrington *et al.*, p. fig. 42.2 [after Walcott 1910, pl. 35, fig. 7 = hypostome questionably assigned to *Arcuolenellus rudis*].
 1959 *Olenellus thompsoni* (Hall); Poulsen in Harrington *et al.*, p. O192, fig. 132a, b.
 1960 *Olenellus thompsoni* (Hall); Kielan, p. 87.
 1960 *Olenellus thompsoni* (Hall); Tchernysheva, p. 62, fig. 32.
 1963 *Olenellus thompsoni* (Hall); Borrello, p. 53.
 not 1968 *Olenellus thompsoni* (Hall); Cowie, p. 14 [citing Raw 1927 and Raymond 1928].
 not 1969 *Olenellus thompsoni* (Hall); Campbell & Kauffman, p. 173, 174, fig. 3 [= *Olenellus getzi* Dunbar 1925 and other Kinzers Formation species].
 1972 *Olenellus thompsoni* (Hall); Fritz (part), p. 11, 15 [references to Vermont material only].
 1973 *Olenellus thompsoni* (Hall); Bergström (part), p. 6 only [not p. 17 = *Olenellus agellus*?, referring to Raw, 1957, text-fig. 5; ?not pl. 1, fig. 1].
 1974 *Olenellus thompsoni* (Hall); Cisne, table 1 (p. 343).
 1978 *Olenellus thompsoni* (Hall); Cowie & McNamara, p. 624.
 1978 *Olenellus (Olenellus) thompsoni* (Hall); McNamara, p. 651.
 1983 *Olenellus thompsoni* (Hall); Speyer, p. 34, 36, fig. 11c?.
 1987 *Olenellus thompsoni* (Hall); Rigby (part), p. 451 only [not caption to fig. 2 = *Olenellus* sp. indet.].
 1989 *Olenellus thompsoni* (Hall); Whittington (part), p. 114–120, 122, 127, 131, 132 [as *Olenellus*], 135, figs 3, 4, 5, 7 only [not p. 125, 137, figs 1, 2, 6, 8, 9, 10, 12, 13, 15, 17, 19, 27, 29, 31, 34 = *Olenellus roddyi*].
 1989 *Olenellus thompsoni* (Hall); Fortey & Whittington (part), p. 131 only [not figs 2, 3 = based on specimens now assigned to *Olenellus roddyi*].
 not 1990 *Olenellus thompsoni* (Hall); Whittington, p. 37 [= *Olenellus roddyi*].
 1992 *Olenellus thompsoni* (Hall); Fritz, p. 10.
 1993 *Olenellus (Olenellus) thompsoni* (Hall); Palmer & Repina, p. 22, fig. 3.1.
 not 1993 *Olenellus thompsoni* (Hall); Babcock, p. 223, figs 2.6, 2.7 [= *Olenellus getzi*].
 1994 *Olenellus thomsoni* [sic] (Hall); Fortey & Theron, p. 856.
 not 1997 *Olenellus thompsoni* (Hall); Whittington in Whittington *et al.*, fig. 45 [= *Olenellus roddyi*].
 1997 *Olenellus (Olenellus) thompsoni* (Hall); Palmer & Repina in Whittington *et al.*, p. 408, fig. 255.1.
 1998b *Olenellus (Olenellus) thompsoni* (Hall); Palmer, p. 668.
 1998 *Olenellus (Olenellus) thompsoni* (Hall); Lieberman, p. 68–70, 71, 72, table 1, fig. 2 [cladogram], 3.1.
 not 1999 *Olenellus thompsoni* (Hall); Yochelson &



- Osborne, fig. 3 [= *Olenellus buttsi*].
 1999 *Olenellus thompsoni* (Hall); Hughes *et al.* (part), table 1 [citing Whittington 1989].
 1999 *Olenellus thompsoni* (Hall); Lieberman (part), p. 3, 13, 15, 17, 19, 25, 27, 28, table 2, table 4, figs 1 [cladogram], 7 [cladogram] only [not p. 41 = *Olenellus* aff. *fowleri*].
 1999 *Olenellus thompsoni* (Hall); Smith & Lieberman, table 1.
 2000 *Olenellus (Olenellus) thompsoni* (Hall); Sundberg, p. 266.
 ?2000 *Olenellus thompsoni* (Hall); Yochelson, p. 320, 322.
 2001 *Olenellus thompsoni* (Hall); Lieberman, p. 101.
 2001 *Olenellus (Olenellus) thompsoni* (Hall); Cotton, p. 170, table 1, table 2.
 2002 *Olenellus thompsoni* (Hall); Lieberman, fig. 2 [cladogram].
 2003 *Olenellus thompsoni* (Hall); Lieberman, table 1.
 not 2003 *Olenellus (Olenellus) thompsoni* (Hall); Babcock, fig. 1.2 [= *Olenellus getzi*].
 2004 *Olenellus thompsoni* (Hall); Dewing *et al.*, p. 1024.
 not 2005 *Olenellus (Olenellus) thompsoni* (Hall); Skinner, p. 172, 179 [= Kinzers Formation species].
 2009 *Olenellus thompsoni* (Hall); Landing *et al.*, p. 562.

Holotype and neotype. The holotype (AMNH 244; Appendix 2) is apparently lost (see Resser & Howell 1938, p. 220; Whittington 1989, p. 114). Two plaster casts of the holotype are in the USNM (USNM 4795 and USNM 62474), and another is in the Walker Museum collection (FMNH UC15942; formerly held at the University of Chicago, now at the Field Museum). For an historical account of these casts see Resser & Howell (1938, p. 217; also Whittington 1989, p. 114). Lieberman (1999, p. 15) designated YPM 8189 as the neotype. The neotype (Lieberman, 1998, fig. 3.1) is an external mould of an individual preserved in a most unusual configuration, with the thorax fractured along the left axial furrow and the left pleurae rotated as an articulated unit away from the remaining trunk. By chance, MW discovered the counterpart internal mould of this specimen in the biological collections of the USNM, and this specimen (USNM 15418c; Fig. 6A) is therefore also the neotype.

Other material. See Appendix 2 for material examined from the Parker Formation. The following cephalons from the Monkton Formation were also examined: FMNH PE58491 (Fig. 7A), FMNH PE58496 (Fig. 7G), FMNH PE58501 (Fig. 7B), FMNH PE58502 (Fig. 7H), NYSM 18376 (Fig. 7C–E), NYSM 18377 (Fig. 7F), NYSM 18378, ICS-10508.7, ICS-10508.29 and ICS-10508.32.

Several other specimens were earlier assigned to *Olenellus thompsoni* but are herein excluded from that species. USNM 90797 (Fig. 13A; also figured by Resser & Howell 1938, pl. 5, fig. 6 as a paratype of “*O. georgiensis*”) was reassigned to *O. thompsoni* by Lieberman (1999, p. 41), but is here reassigned to *O. aff. fowleri* (below). USNM 15419a from the “magnesian limestone” (likely the Dunham Formation) east of Swanton, Vermont, was previously figured as *O. thompsoni* (see Appendix 2) but is herein treated as *O. sp.* indeterminate. Lieberman (1998,

1999) also assigned MCZ 2460, MCZ 2467, MCZ 2469 and tentatively MCZ 2482 to *O. thompsoni*. However, MCZ 2460 is too poorly preserved for specific identification, and MCZ 2469 (a lot of two specimens) and MCZ 2482 all possess a preglabellar field and are herein reassigned to *O. agellus*. A preglabellar field might also have been present on the poorly preserved MCZ 2467, and this specimen is here reassigned to *O. cf. agellus*.

Several more specimens have been previously assigned to *Olenellus thompsoni*, but none of these were examined during the course of the present study nor have they been figured in the literature. As a result, their taxonomic assignment cannot be confirmed. See Appendix 2 for details.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25 and the effectively equivalent USNM Locality 319m, within the Parker Formation. Powerline section, Chittenden County: ICS-10507 and ICS-10508, in the middle Monkton Formation. Colchester, Chittenden County: Unknown horizon within the Monkton Formation.

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin directed weakly posteriorly by up to 10° relative to a transverse line (more or less transversely oriented on largest specimen; Fig. 6C, D), distal portion flexed anteriorly by approximately 20–30° relative to proximal portion at rounded intergenal angle located approximately 81–89% of distance from axial furrow to base of genal spine. Greatest observed cephalic length estimated to exceed 41 mm (sag.; Fig. 6C). Genal spine slender, base transversely opposite or behind posterior margin of LO; length approximately 30–45% cephalic length (sag.). Distance (tr.) between genal spine bases approximately 165–225% of cephalic length (sag.), distance generally proportionally increases during ontogeny. Intergenal spine retained as small spine on posterior cephalic border immediately distal to intergenal angle; length less than half that (exsag.) of LO. Cephalic border well defined around entire cephalon by distinct border furrow; rises relatively steeply out of border furrow, then gently slopes down to cephalic margin as flattened surface; width of anterior border opposite junction of ocular lobes with LA approximately 7–10% length (exsag.) of glabella. Anterior margin of LA contacts anterior border furrow at sagittal line; preglabellar field absent. Glabella weakly constricted at S1; approximately 87–95% cephalic length (sag.; perhaps increasing slightly through sampled portion of ontogeny). Maximum width of LA approximately 104–119% basal glabellar width (tr.). Posterior margin of glabella very weakly convex posteriorly to more or less transverse. SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subquadrate to subtrapezoidal, slightly narrows anteriorly, length (exsag.) approximately 14–17% glabellar length (sag.). S1 deepest abaxially, approximately parallel to SO. L1 subtrapezoidal, slightly narrows anteriorly; length (exsag.) approximately 13–17% glabellar length (sag.). Lateral margins of LO and L1 bow slightly outward. S2 and S3 shallower than SO and S1. S2 deepest midway between sagittal line and axial furrow, isolated from axial

Figure 7. Cephalons of *Olenellus thompsoni* from the Monkton Formation. **A**, FMNH PE58491, dorsal view, x4. **B**, FMNH PE58501, dorsal view, x6. **C–E**, NYSM 18376 in dorsal, right lateral, and oblique anterodorsolateral views, respectively, x2. **F**, NYSM 18377, dorsal view, x2. **G**, FMNH PE58496, dorsal view, x3. **H**, FMNH PE58502, dorsal view, x3. All internal moulds. A from ICS-10507, Powerline section, Chittenden County, Vermont. B, G, H from ICS-10508, Powerline section, Chittenden County, Vermont. C–F from Colchester, Chittenden County, Vermont.

furrow, abaxial end slightly anterior to adaxial end. L2 widens anteriorly; anterolateral portion confluent with posterolateral portion of L3. S3 directed anterolaterally away from axis until intersection with ocular lobes, deepest midway between sagittal line and axial furrow, retains very shallow connection to axial furrow in some specimens (Fig. 6B, C). L3 broadly 'M'-shaped; distal tips of L3 poorly defined by very shallow axial furrow. LA subcircular in outline, 75–97% as long (sag.) as wide (tr.), approximately 46–50% glabellar length (sag.), becomes proportionally longer through sampled portion of ontogeny, weakly convex and not prominently inflated relative to extraocular area (Fig. 7C–E); widest point at intersection with anterior margin of ocular lobes. Tiny axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at 8–17°, crescentic, flat-topped; posterior tip transversely opposite anterior third of lateral margin of LO. Very shallow ocular furrow on anterior part of ocular lobe, inner band wider (tr.) than outer band. Interocular area shelf-like to gently arched in transverse section, approximately as wide (tr.) as ocular lobes and 25–60% width (tr.) of extraocular area opposite S1 (decreasing over sampled portion of ontogeny as extraocular area proportionally widens). Extraocular genal caeca (Fig. 6B–D), weak posterior ocular line (Fig. 6B, D), and genal ridge (Fig. 6D) present on some specimens. Bertillon markings on lateral and anterior cephalic border (Fig. 6B, C) and entire dorsal surface of glabella (Fig. 6B, D), become subreticulate over sagittal line (Fig. 6B, D); one specimen shows Bertillon markings on extraocular area, interocular area and ocular lobes (Fig. 6C, D), with markings becoming subreticulate adaxially. Terrace lines or lirae on cephalic doublure (Fig. 6C).

Rostral plate narrower (sag.) than anterior and lateral cephalic border, crescentic; abaxial ends curve to point slightly medially in plan view (Fig. 6B). Hypostome unknown.

Prothorax of 14 segments; width (tr.) of axis approximately 88% (range 84–93%) width (tr.) of inner pleural region on T1, gently tapers posteriorly. Small axial node consistently present on all prothoracic segments, that on T14 larger and spinelet-like. Inner pleural regions of T1 and T2 transverse, parallel-sided (Fig. 6C) to slightly tapered distally, with straight margins; pleural spines of T1 and T2 slender, divergent, sentate to weakly falcate, pleural spine of T2 slightly longer than that of T1. T3 macropleural (less strongly so on largest specimen; Fig. 6C); pleural spine macrospinous with posterior tip located transversely opposite axial ring of T7 or T8 (Fig. 6A), T9 (Fig. 6C), or T10 (Fig. 6B). Inner pleural region of T4 transverse, slightly tapers distally to accommodate macropleural T3, with straight margins; inner pleural regions of T5–T10 transverse, parallel-sided, with straight margins; those of more posterior prothoracic segments increasingly divergent to pendent, with increasingly curved margins. Pleural spines of T4 slender, weakly falcate; those of T5–T14 falcate, progressively increasing in length posteriorly along the prothorax to T12 or T13 then proportionally decreasing in length on more posterior prothoracic segments, transitioning from divergent to pendent to sometimes slightly convergent on T9–T14. Pleural furrows of all prothoracic segments wide (exsag.), occupying much of inner pleural region, anterior wall steeper than posterior wall; extending onto pleural spines of T3–T14 (also T1 and T2 on largest specimen; Fig. 6C). Bertillon markings on axial ring of all prothoracic segments, becoming

reticulate over sagittal line (Fig. 6D). Antero-posteriorly oriented Bertillon markings on inner pleural regions of all prothoracic segments on at least one specimen (Fig. 6C, D). Lirae or terrace lines grade to Bertillon markings on ventral surface of pleural spine of all prothoracic segments.

Opisthothorax with four segments (T15 to T18; Fig. 6C, E). Long, slender, axial spine on T15 (full length unknown, but at least half the length of entire prothorax), base as wide as T15 axis; presence or absence of axial structures on more posterior segments unknown (obstructed by T15 axial spine). Axes of all segments poorly defined by break in slope; axial furrows not incised. Inner pleural regions much narrower than axes (tr.); margins curved, converging into short, weakly divergent to pendent, sentate pleural spines. Pleural furrows not evident. Axial spine of T15 sometimes bears reticulate ornament (Fig. 6E). Bertillon markings on axis and pleural regions of all opisthothoracic segments.

Pygidium tiny (Fig. 6C, E), length less than 10% that of cephalon (sag.); subquadrate; lateral margins curve smoothly into single pair of lobate extensions at posterolateral corners; posterior margin with median notch between lobate extensions. Axis very weakly defined (especially anteriorly) by break in slope, triangular, tapers posteriorly to blunt point, terminates slightly anterior to posterior pygidial margin; segmentation unclear but possibly consists of one segment plus terminal piece. Pleural field slopes down to pygidial margin, pygidial border not defined.

Remarks. *Olenellus thompsoni* has been regarded as “the reference point for discussions of olenellid anatomy” (Fortey & Theron 1994). The species has been used as an exemplar for broader clades in cladistic analyses (Lieberman 1998, 2001; Cotton 2001) and for early Cambrian trilobites in textbooks (e.g., Boardman *et al.* 1987, fig. 13.21i; Black 1989, fig. 93a; Valentine 2004, fig. 7.29a). It has also been used in palaeobiological analyses (Hughes *et al.* 1999; Smith & Lieberman 1999). It is therefore important to accurately characterise the morphology of the species.

Whittington (1989) provided a detailed description of *Olenellus thompsoni* and found that the species exhibited variation in several traits, including opisthothoracic segment number (four or five). Whittington's (1989) segmentation data were subsequently incorporated into a broader analysis of intraspecific variation in trilobites (Hughes *et al.* 1999, table 1). However, Whittington's (1989) description is unfortunately compromised because it was based, in part, on specimens now assigned to *O. transitans*, *O. getzi* Dunbar 1925 and *O. rodnyi* Resser & Howell 1938 (Lieberman 1998, 1999; also herein), and much of the supposed intraspecific variation in *O. thompsoni* is now recognised as interspecific disparity. For example, *O. thompsoni* apparently possessed only four opisthothoracic segments (see above), with the five-segmented specimens being *O. rodnyi*. (This revision does not materially affect the conclusions drawn by Hughes *et al.* [1999, table 1], because intraspecific variation in thoracic segment number has since been documented in two other olenelloid species [Webster 2015, p. 65].) Differences between *O. thompsoni*, *O. transitans*, *O. getzi* and *O. rodnyi* were clarified by Lieberman (1998, 1999; also herein). Differences between *O. thompsoni* and *O. agellus* are discussed under the latter species.

This report reveals several errors and inconsistencies in the character coding of *Olenellus thompsoni* by Lieberman

(1998, 1999). The lateral margins of LA (Lieberman 1998, character 11) were coded as being directly anterior to the lateral margins of LO (state 2) by Lieberman (1998), but were subsequently coded as being distal to the lateral margins of LO (equivalent to state 1) by Lieberman (1999, Olenellinae analysis, character 4, Mesonacinae analysis, character 16). The latter state is deemed accurate. The ocular lobe is separated from the extraocular area by a distinct eye socle (Fig. 6C, D, 7C–E; Lieberman 1998, character 16, state 0); this had been coded by Lieberman (1998) as merging smoothly into the extraocular area (state 0). The divergence of the ocular lobes from an exsagittal line (Lieberman 1998, character 20) was coded as forming a 10–20° angle with the sagittal line (state 0) by Lieberman (1998), and as forming a 0–5° angle (equivalent or closely so to state 1) by Lieberman (1999, Mesonacinae analysis, character 18). The former state is deemed more accurate. The transverse profile of the interocular area (Lieberman 1998, character 22) is shelf-like to gently arched (polymorphic; states 1 and 2); this had originally been coded as shelf-like (state 1). The posterior margin of LO (Lieberman 1998, character 41) is variably transverse to weakly convex posteriorly (states 0, 1; compare Fig. 6C to Fig. 6A or Fig. 7C); this had originally been coded as roughly transverse (state 0). Extraocular genal caeca (Lieberman 1998, character 45) are present (state 0; Fig. 6C, D); these had originally been coded as absent (state 1). An intergenal ridge (Lieberman 1998, character 48) was not observed on any specimen (state 1); this had originally been coded as being visible as a trace (state 0). The posterior cephalic margin between the axial furrow and intergenal angle (Lieberman 1998, character 56; Lieberman 1999, Mesonacinae analysis, character 15) is variably transverse to weakly posteriorly oriented (states 0, 1); this had originally been coded as posteriorly oriented (state 1) by Lieberman (1998, 1999). Any dorsoventral sloping of the tips of the thoracic pleurae (Lieberman 1998, character 71) cannot be determined because all available thoracic material has experienced taphonomic compaction; this had originally been coded as being in roughly the same dorsoventral plane as medially (state 2). The length of the axial spine on T15 (Lieberman 1998, character 74) is unknown; this had originally been coded as being as long as the whole prothorax (state 1). The length:width ratio of the pygidium (Lieberman 1998, character 78) had originally been coded as being approximately 1.5 (state 0), but is actually much closer to 1.0 (state 1; Fig. 6E). The posterior margin of the pygidium (Lieberman 1998, character 79) bears a median notch (state 1; Fig. 6E); this had originally been coded as being transverse or weakly convex (state 0). Finally, the genal spine (Lieberman 1999, Mesonacinae analysis, character 6) was coded as being approximately 4–5 times the length (sag.) of LO (state 0), but a value of approximately twice the length (sag.) of LO (state 2) appears to be more accurate.

Specimens of *Olenellus thompsoni* examined herein range from approximately 6.6 mm (Fig. 7B) to 41 mm (Fig. 6C) in sagittal cephalic length. Most are relatively large individuals well into phase 5 of cephalic development. Some allometry is evident in the species' ontogeny. Most noticeable is the proportional widening of the extraocular area. Also evident is a proportional elongation of LA. On all specimens examined herein a preglabellar field is absent because the anteriormost margin of LA contacts the anterior border furrow at the sagittal line (although LA does not impinge into the border furrow or deflect the course

of either the border furrow or the border). However, LA progressively lengthens through ontogeny and, if this trend were to be extrapolated to smaller (unsampled) specimens, it is conceivable that a short preglabellar field was present on morphologically immature cephalia. Other olenelloid species are known to have experienced a progressive decrease in the size (and sometimes ultimate loss) of the preglabellar field through late stages of ontogeny (e.g., *O. gilberti* Meek in White 1874 and *Nephrolenellus multinodus* [Palmer in Palmer & Halley 1979]; Webster 2007a, 2015). Resolution of whether or not the lack of a preglabellar field on mature cephalia of *O. thompsoni* reflects a primary absence or a secondary loss will require the discovery of smaller specimens.

***Olenellus transitans* (Walcott 1910) (Figs 8, 9)**

- ?1861 *Barrandia vermontana* (Hall); Hall (part), p. 370, reference to pl. 13, figs 4, 5 only [= *Olenellus transitans* or *Olenellus brachycephalus*].
 ?1862a *Barrandia vermontana* (Hall); Hall (part), pl. 13, figs 4, 5 only [= *Olenellus transitans* or *Olenellus brachycephalus*].
 1884 *Olenellus thompsoni* (Hall); Whitfield (part), pl. 15, figs 1, 2, 3? only.
 1910 *Paedeumias transitans*; Walcott (part), p. 305–310, pl. 34, fig. 1 only [not pl. 24, fig. 12 = *Olenellus thompsoni*; not pl. 25, figs 19–22 = *Olenellus* sp. indet.; not pl. 32, figs 1–5, 9, 11, 12 = *Olenellus*? sp. indet.; not pl. 32, fig. 6 = *Olenellus glabrum*?; not pl. 32, figs 7, 8, 10, 13 = *Olenellus rodnyi*; not pl. 33, fig. 1 = *Olenellus thompsoni*; not pl. 33, figs 2–5 = *Olenellus*? sp. indet.; not pl. 34, figs 2–4, 6 = *Olenellus rodnyi*; not pl. 34, figs 5, 7, 8 = indet. hypostomes; not pl. 44, fig. 7 = *Olenellus thompsoni*].
 1912a *Paedeumias transitans* Walcott; Walcott (part), p. 188 only [?not p. 147, 206].
 not 1912b *Paedeumias transitans* Walcott; Walcott, p. 246 [= Kinzers Formation species].
 not 1927 *Paedeumias transitans* Walcott; Poulsen, text-fig. 7 (p. 312) [= *Olenellus rodnyi*].
 1928 *Paedeumias transitans* Walcott; Resser, p. 4.
 1931 *Olenellus thompsoni* (Hall); Bell, fig. 4.
 1936 *Paedeumias transitans* Walcott; Grabau (part), p. 27, 124 only [?not p. 14].
 1937 *Paedeumias transitans* Walcott; Schuchert, p. 1026.
 ?not 1937 *Paedeumias transitans* Walcott; Öpik, p. 130, fig. 39 [= *Olenellus rodnyi*?].
 1938 *Paedeumias transitans* Walcott; Resser & Howell, p. 226, pl. 8, fig. 13.
 1938 *Paedeumias perkinsi*; Resser & Howell, p. 226, pl. 8, fig. 1.
 1938 *Olenellus agellus*; Resser & Howell (part), pl. 9, fig. 11 only.
 1944 *Paedeumias transitans* Walcott; Shimer & Shrock, p. 615, pl. 254, fig. 18.
 not 1952 *Paedeumias (Olenellus) transitans* Walcott; Hupé, p. 276 [= referring to Walcott 1910, pl. 34, figs 7, 8 = indet. hypostomes].
 1953 *Paedeumias transitans* Walcott; Hupé (part), fig. 51.1 only [not p. 90, 91, 101, figs 48, 49 (7, 8) = *Olenellus* sp. indet. and *Olenellus rodnyi*].
 not 1953 *Paedeumias transitans* Walcott; Raw, p. 96 [= *Olenellus rodnyi*].
 1954 *Olenellus brachycephalus* (Emmons); Shaw, p. 1041.
 1955 *Olenellus brachycephalus* (Emmons); Shaw, p. 791,

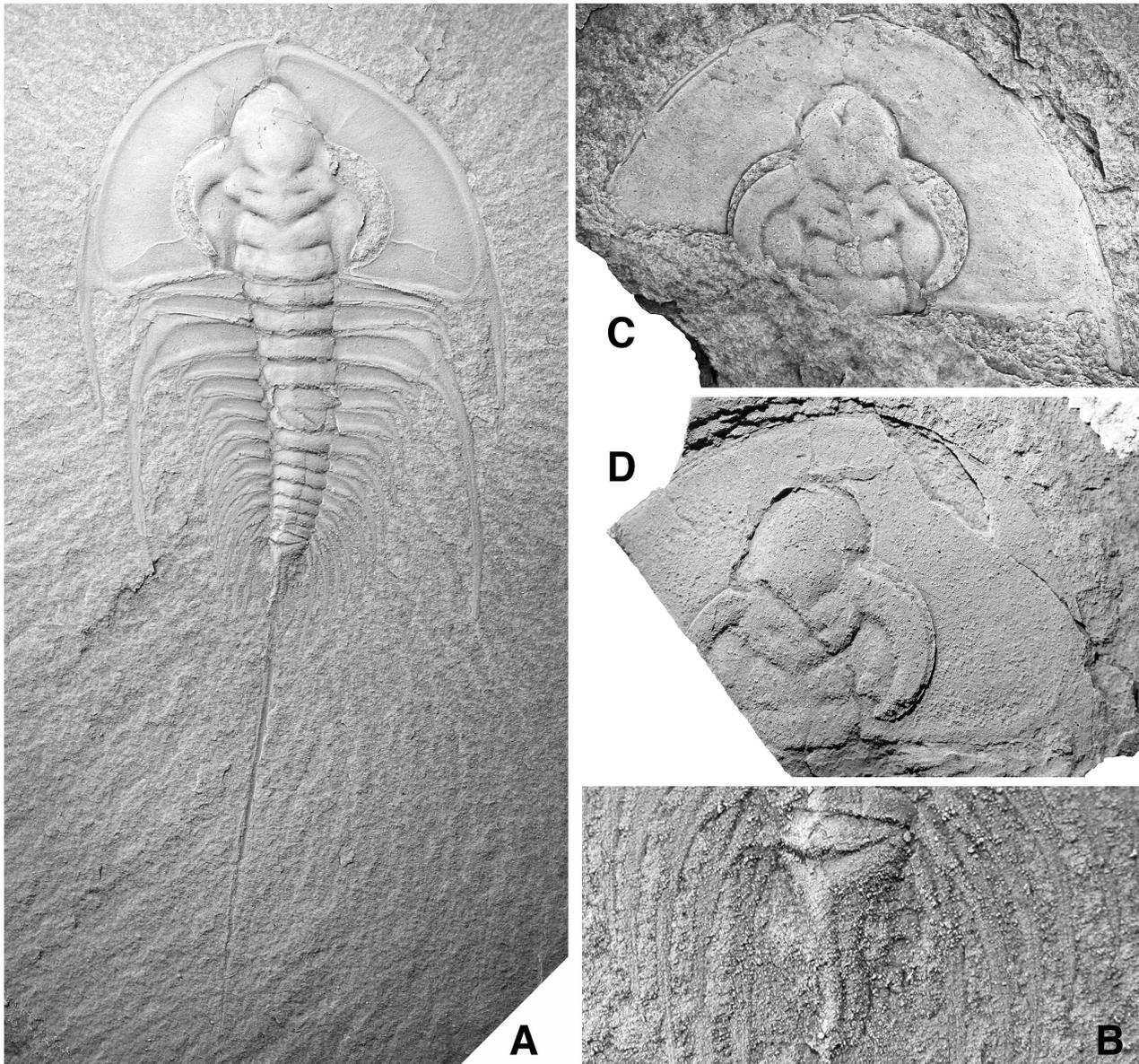


Figure 8. *Olenellus transitans* from the Parker Formation. **A, B**, USNM 56808b (lectotype). **A**, complete dorsal exoskeleton, x3. **B**, details of opisthothorax, x10. **C**, cephalon, internal mould, MCZ 52525, x1.5. **D**, cephalon, internal mould, MCZ 108661, x2. All in dorsal view. **A, B** from Parker quarry, Franklin County, Vermont. **C** from Locality 4789, Franklin County, Vermont. **D** from Kelly Quarry, Franklin County, Vermont.

- 792, pl. 75, figs 1–3.
 1956 *Paedeumias transitans* Walcott; Lochman, p. 1354.
 1957 *Paedeumias transitans* Walcott; Raw, p. 172.
 not 1957 *Paedeumias transitans* Walcott; Palmer, p. 120 [referring to Walcott 1910, pl. 25, figs 19–22, pl. 32, figs 1–8], 126 [referring to Walcott 1910, pl. 34, figs 6, 7].
 1959 *Paedeumias transitans* Walcott; Harrington in Harrington *et al.* (part), fig. 48c only [not p. O114 = *Olenellus rodnyi*].
 1959 *Paedeumias transitans* Walcott; Poulsen in Harrington *et al.*, p. O192, fig. 135.5.
 1960 *Paedeumias transitans* Walcott; Tchernysheva, p. 62, fig. 33.
 1968 *Paedeumias transitans* Walcott; Cowie, p. 13, 14.
 not 1975 *Paedeumias transitans* Walcott; Henningsmoen, p. 192, fig. 9.3 [= *Olenellus rodnyi*].
 1978 *Olenellus transitans* (Walcott); Cowie & McNamara, p. 624.
 1983 *Paedeumias transitans* Walcott; Lauterbach, fig. 3b. not 1983 *Olenellus (Paedeumias) transitans* (Walcott); Stouge & Boyce, p. 19, pl. 8, fig. 5 [= *Olenellus* n. sp.?].
 1993 *Olenellus (Paedeumias) transitans* (Walcott); Palmer & Repina, p. 22, 23, fig. 3.3.
 1997 *Olenellus (Paedeumias) transitans* (Walcott); Palmer & Repina in Whittington *et al.*, p. 408, fig. 255.3.
 1998 *Olenellus (Paedeumias) transitans* (Walcott); Lieberman, p. 62, 66, 68, 70, table 1, figs 2 [cladogram], 3.2, 3.3.
 1999 *Olenellus transitans* (Walcott); Lieberman, p. 13, 15, 17?, 19, 20, 27, table 2, fig. 1 [cladogram].
 1999 *Olenellus transitans* (Walcott); Smith & Lieberman, table 1.
 2000 *Olenellus (Paedeumias) transistans* [sic] (Walcott); Sundberg, p. 266.



Figure 9. *Olenellus transitans* from the Parker Formation. **A**, latex peel of internal mould, PUM 42012, x0.9. **B**, tentatively assigned cephalon, latex peel of external mould, MCZ 2478a, x2. Both in dorsal view. A from unknown locality, Vermont. B from Parker quarry, Franklin County, Vermont.

2001 *Olenellus transitans* (Walcott); Lieberman, p. 101.

2002 *Olenellus transitans* (Walcott); Lieberman, fig. 2 [cladogram].

2003 *Olenellus transitans* (Walcott); Lieberman, table 1.

Lectotype. USNM 56808b (Fig. 8A, B), designated by Resser (1928, p. 4).

Other material. See Appendix 2. USNM 14675.236a is a lot of two specimens. Confusingly, Lieberman (1999) included the specimen figured by Resser & Howell (1938, pl. 9, fig.

11) under the synonymy of both *O. transitans* (p. 15) and *O. agellus* (p. 17)—that specimen is herein assigned to *O. transitans*. The second specimen in the collection (an external mould) has never been figured and is too poorly preserved for species-level identification. Several other specimens listed as representing *Olenellus transitans* by Lieberman (1998, p. 70; 1999, p. 15) probably do represent *O. transitans* but are poorly preserved and therefore contributed no data to the description. These specimens are: MCZ 2428 (3 slabs), MCZ 2431 (2 slabs), MCZ 2433 (a specimen with the same number was also assigned to *O. agellus* by Lieberman 1999, p. 17), MCZ 2437 (2 slabs), MCZ 2438 (3 slabs), MCZ 2444, MCZ 2447 (2 slabs), MCZ 2449 (3 slabs), MCZ 2450 (5 slabs), MCZ 2453 (3 slabs), MCZ 2455 (2 multispecimen collections), MCZ 2461 (2 multispecimen collections), MCZ 2474, MCZ 2480 (3 slabs, 2 multispecimen collections), MCZ 2522 (5 slabs) and MCZ 7368. Several more specimens were not examined during this study and thus form no part of the species description, but published illustrations indicate that they should be assigned to *Olenellus transitans*. These specimens are AMNH 223, AMNH 227 and an unspecified AMNH specimen (see Appendix 2).

Other specimens have been assigned to *Olenellus transitans* by earlier authors but have never been figured and were not examined in this study. The assignment of these specimens to *O. transitans* is therefore not confirmed. Several more specimens were assigned to *Olenellus transitans* by Lieberman (1998, p. 70; 1999, p. 15), but examination of specimens or scrutiny of illustrations in this study indicate that the specimens were either misassigned or cannot be identified to species level. See Appendix 2 for details.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25 and the effectively equivalent USNM Locality 319m, within the Parker Formation. Kelly quarry, Franklin County: within the Parker Formation. Locality 4789, Franklin County: within the Parker Formation. Several specimens in museum collections are simply labelled as being collected from “Georgia, Vermont” or bear no locality information at all. The lithology of the slabs is consistent with these specimens having been collected from the Parker Formation.

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin directed weakly posteriorly at 2–11°, distal portion flexed anteriorly by approximately 9–35° relative to proximal portion at intergenal angle located approximately 65–83% of distance from axial furrow to base of genal spine. Greatest observed cephalic length estimated to exceed 51 mm (sag.; Fig. 9A). Genal spine slender, base transversely opposite posterior or middle portion of lateral margins of LO; length approximately half that of cephalon (sag.; Fig. 8A). Distance (tr.) between genal spine bases 138–159% (possibly up to 173%; Fig. 9B) of cephalic length (sag.). Short, pointed, intergenal spine on posterior cephalic border immediately distal to intergenal angle; length approximately half that (exsag.) of LO. Cephalic border well defined around entire cephalon by distinct border furrow, flattened; width of anterior border opposite junction of ocular lobes with LA approximately 7–10% length (exsag.) of glabella. Preglabellar field moderately long, sagittal length typically two to three times width of anterior cephalic border, proportionally decreasing slightly over sampled portion

of ontogeny (less than twice width of anterior border on tentatively assigned YPM 72900 and MCZ 2478a; Fig. 9B). Plectrum present, often narrow and faint. Glabella weakly constricted at S1; 76–85% cephalic length (sag.), proportionally slightly lengthens over sampled portion of ontogeny at expense of preglabellar field. Maximum width of LA approximately 87–112% (average 102%) basal glabellar width (tr.). Posterior margin of glabella weakly convex posteriorly. SO deep only abaxially, directed weakly posteriorly or more or less transversely inwards (Fig. 8C, D). LO subrectangular to subtrapezoidal, slightly narrows anteriorly, length (exsag.) 13–17% glabellar length (sag.). S1 deepest abaxially, slightly more strongly posteriorly directed inwards than SO. L1 subtrapezoidal, narrows anteriorly; length (exsag.) 14–17% glabellar length (sag.). Lateral margins of LO and L1 bow slightly outward. S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, abaxial end slightly anterior to adaxial end. L2 widens anteriorly; anterolateral portion confluent with posterolateral portion of L3. S3 deepest midway between sagittal line and axial furrow, isolated from axial furrow, directed anterolaterally away from axis until contact with ocular lobes. L3 broadly 'M'-shaped; axial furrow slightly shallower at distal tips of L3. LA subovate in outline, approximately 91–118% (average 105%) as long (sag.) as wide (tr.), approximately 47–52% glabellar length (sag.), separated from extraocular area by a sharp break in slope, weakly convex and not prominently inflated relative to extraocular area (although precise dorsal convexity and degree of inflation are uncertain due to compaction); widest point at contact with anterior margin of ocular lobes. Tiny axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at 6–17°, crescentic, flat-topped; posterior tip transversely opposite posterior or anterior half of lateral margin of LO. Extremely shallow ocular furrow sometimes developed; deepest anteriorly when present, inner band slightly wider (tr.) than outer band (Fig. 8C). Interocular area weakly arched in transverse profile on some specimens (Figs 8C, 9B; also FMNH 23259, MCZ 2478b) but appears flat-topped on others, approximately 83–141% (average 103%) as wide (tr.) as ocular lobes and 24–54% (average 33%) width (tr.) of extraocular area opposite S1. Genal ridge and weak extraocular genal caeca on some specimens (Fig. 8A); posterior ocular line present on one tentatively assigned specimen (Fig. 9B). Terrace lines on cephalic doublure (Fig. 8A, C, D) and genal spines (Fig. 8C, D). Rostral plate and hypostome unknown.

Prothorax of 14 segments; width (tr.) of axis approximately 80–92% width (tr.) of inner pleural region on T1, gently tapers posteriorly. Small axial node or spinule consistently present on posterior prothoracic segments from T8 (Fig. 8A) to T14, increases in size posteriorly from axial swellings or small nodes to axial spinelets; axial node or spinelet present on T1 and T2 on at least some specimens (Fig. 8A); axial structure on T3–T7 either not developed or perhaps represented by minuscule spinelet (Fig. 8A). Inner pleural regions of T1 and T2 transverse, slightly taper distally (particularly T1), with straight margins; pleural spines of T1 and T2 slender on small specimens (slightly broader on larger specimens), divergent, sentate to weakly falcate (proportionally longer on larger specimens), pleural spine of T2 slightly longer than that of T1. T3 macropleural (weakly so on larger specimens); pleural spine dolichospinous with posterior tip extending beyond entire trunk on smallest specimen (Fig. 8A), total length

unclear on larger specimens. Inner pleural region of T4 transverse, slightly tapers distally, with slightly curved anterior margin to accommodate distal expansion of T3; inner pleural regions of T5–T9 transverse, parallel-sided, with straight margins; those of more posterior prothoracic segments increasingly divergent to subpendent, with increasingly curved margins. Pleural spines of T4 slender, divergent, sentate to weakly falcate (becoming more strongly falcate on larger specimens); those of T5–T14 falcate, progressively increase in length down the prothorax, transition from divergent to subpendent on T9–T14. Pleural furrows of all prothoracic segments wide (exsag.), occupying much of inner pleural region, anterior wall steeper than posterior wall; extend onto pleural spines of all prothoracic segments. Lirae or terrace lines on pleural spines of at least T2–T4 and T14 on some specimens (MCZ 2459).

Opisthothorax known from lectotype only (Fig. 8A, B); poorly preserved, consists of at least four segments. Long, slender, axial spine on T15 (length longer than entire prothorax [sag.]), base as wide as T15 axis; presence or absence of axial structures on more posterior segments cannot be determined. Right pleurae of at least four segments visible posterior to axial ring of T15; it is unclear whether the anteriormost of these pleurae belongs to T15 or T16, so these segments represent either T15–T18 or T16–T19. Pleurae poorly developed; posterior margins curve into short, weakly divergent to pendent, sentate pleural spines. Pleural furrows not evident. Axes of these segments obscured by T15 axial spine. Axial spine of T15 possibly bears granular ornament. Small exoskeletal fragment immediately posterior to right pleura of T18/T19 represents right anterolateral portion of either another opisthothoracic segment (T19 or T20) or pygidium.

Remarks. Shaw (1955) considered *Paedeumias transitans* to be a junior synonym of *Olenellus brachycephalus*. Lieberman (1998, p. 70) noted that the type material of *O. brachycephalus* is lost, and this putative synonymy therefore cannot be verified. Lieberman (1998, p. 70) proposed that the status of *O. brachycephalus* is indeterminate, with which we concur.

In agreement with Shaw (1955) and Lieberman (1998, 1999), *Paedeumias perkinsi* is herein regarded as a junior subjective synonym of *Olenellus transitans*. Resser & Howell (1938, p. 226) stated that *P. perkinsi* differed from *O. transitans* in having a longer preglabellar field and a narrower thorax. Shaw (1955, p. 792) believed that these represented arbitrarily separated variants, and synonymised *P. perkinsi* with *O. brachycephalus*. Lieberman (1998, 1999) restricted *O. brachycephalus* to the (lost) type specimen, but followed Shaw in considering *P. perkinsi* to be a junior synonym of *O. transitans*. Three specimens of *P. perkinsi* were examined in this study, ranging from 24.6 mm to approximately 29 mm in sagittal cephalic length. These fall within the sampled size range of “typical” *O. transitans* (sagittal cephalic length ranging from approximately 12 mm to 51 mm). The glabellae of the three specimens of *P. perkinsi* measure 78–82% of their sagittal cephalic length, and the glabellae of *O. transitans* ranges from 76% to 85% of the sagittal cephalic length (lectotype = 82%). There is therefore no justification for treating *P. perkinsi* as distinct from *O. transitans*.

Olenellus transitans is very similar to the co-occurring taxon *O. agellus* (Fig. 11) and to the poorly known



Figure 10. *Olenellus* aff. *transitans* from the Parker Formation, Parker quarry, Franklin County, Vermont. Cephalon and incomplete prothorax, internal mould, USNM 56808a, dorsal view, x4.

Cordilleran species *O. puertoblancoensis*. Differences between *O. transitans* and *O. agellus* are discussed under the latter species. *Olenellus transitans* seems to differ from *O. puertoblancoensis* in terms of ocular lobe length (proportionally slightly longer in *O. puertoblancoensis*) and cephalic outline (the posterior cephalic margin being straighter in *O. puertoblancoensis*). A detailed investigation of *O. puertoblancoensis*, based in part on newly collected material, is currently under way. The results of that investigation will shed light on the validity of the distinction between *O. transitans* and *O. puertoblancoensis*.

This study has revealed several issues with the coding of *Olenellus transitans* in the phylogenetic analyses presented by Lieberman (1998, 1999). The maximum width of LA ranges from slightly narrower to slightly wider than the basal glabella width (Lieberman 1998, character 11, states 0, 1, 2); this had originally been coded as narrower (state 0; see also Lieberman 1999, Olenellinae analyses, character 4; Lieberman 1999, Mesonacinae analyses, character 16 coded this as directly anterior to the lateral margins of LO). An eye socle is present and forms a distinct lip that separates the ocular lobe from the extraocular area (Fig. 8A, C, D; Lieberman 1998, character 16, state 0); the ocular lobe had originally been coded as merging smoothly into the extraocular area (state 1). An ocular furrow (Lieberman 1998, character 19) is extremely shallow but nevertheless present on at least some specimens (Fig. 8C). Whether this condition is considered “prominent” (state 0) or “not prominent” (state 1, as originally coded) is debatable. The surface of the interocular area (Lieberman 1998, character 22) is slightly arched (state 2) on at least some specimens (Figs 8C, 9B); this had originally been coded as being developed as a flattened shelf (state 1). An axial node is

present on the posterior margin of LO on at least some specimens (Fig. 8D; Lieberman 1998, character 40, state 0); this had originally been coded as absent (state 1). The posterior margin of LO (Lieberman 1998, character 41) is weakly convex posteriorly (state 1); this had originally been coded as transverse (state 0). The original convexity of the extraocular area (Lieberman 1998, character 44) cannot be determined because all material has experienced compactional deformation. It had originally been coded as being flattened (state 0; see also Lieberman 1999, Olenellinae analysis, character 10). Extraocular genal caeca are present on at least some specimens (Fig. 8A; Lieberman 1998, character 45, state 0) but had originally been coded as absent (state 1). An intergenal ridge (Lieberman 1998, character 48) was not seen on any specimen (state 1); this had originally been coded as being visible as a trace (state 0). The proximal portion of the anterior margin of the pleural furrow on T3 (Lieberman 1998, character 61) is variably either transversely (Fig. 8A) or weakly posteriorly directed (MCZ 2459) when traced distally (states 0 and 1); this was originally coded as being transversely oriented (state 1). The dorsoventral flexure of the distal tips of the thoracic segments (Lieberman 1998, character 71) cannot be determined because all material has experienced compactional deformation. It had originally been coded as being in roughly the same plane as medially (state 0). An unambiguous pygidium was not seen on any specimen examined in this study; accordingly, pygidial characters should be treated as state unknown (Lieberman 1998, characters 78, 79). Lieberman (1998) coded the pygidium as being relatively narrow (character 78, state 0) and with a transverse or weakly convex posterior margin (character 79, state 0).

Olenellus* aff. *transitans (Walcott 1910) (Fig. 10)

Material. USNM 56808a, a single specimen co-occurring on the same slab as a large external mould of *Olenellus thompsoni*.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25 or the effectively equivalent USNM Locality 319m, within the Parker Formation.

Remarks. The single specimen of *Olenellus* aff. *transitans* (Fig. 10) has a sagittal cephalic length of approximately 10.1 mm, and is therefore slightly smaller than the lectotype of *O. transitans* (Fig. 8A, sagittal cephalic length approximately 12.2 mm). *Olenellus* aff. *transitans* differs from the lectotype of *O. transitans* in having proportionally slightly longer ocular lobes that appear to be less strongly divergent from the sagittal line, slightly narrower interocular areas, a slightly straighter posterior cephalic margin (with a weaker intergenal angle), and possibly also a slightly narrower cephalic border (although the anterior and lateral cephalic margins are worn on *O. aff. transitans*). *Olenellus* aff. *transitans* also possesses slightly less strongly tapered pleurae on T1, and bears a tiny axial spinelet on the posterior margin of T3 (perhaps absent on the lectotype of *O. transitans*, although the posterior margin of the T3 axial ring is not well preserved on that specimen). These differences might result from interspecific disparity, ontogenetic allometry, intraspecific variation, and/or differences in taphonomic compaction. The straighter posterior cephalic margin and longer ocular lobes of *O. aff. transitans* are also reminiscent of *O. puertoblancoensis* (see above). A study of the latter will shed light on the

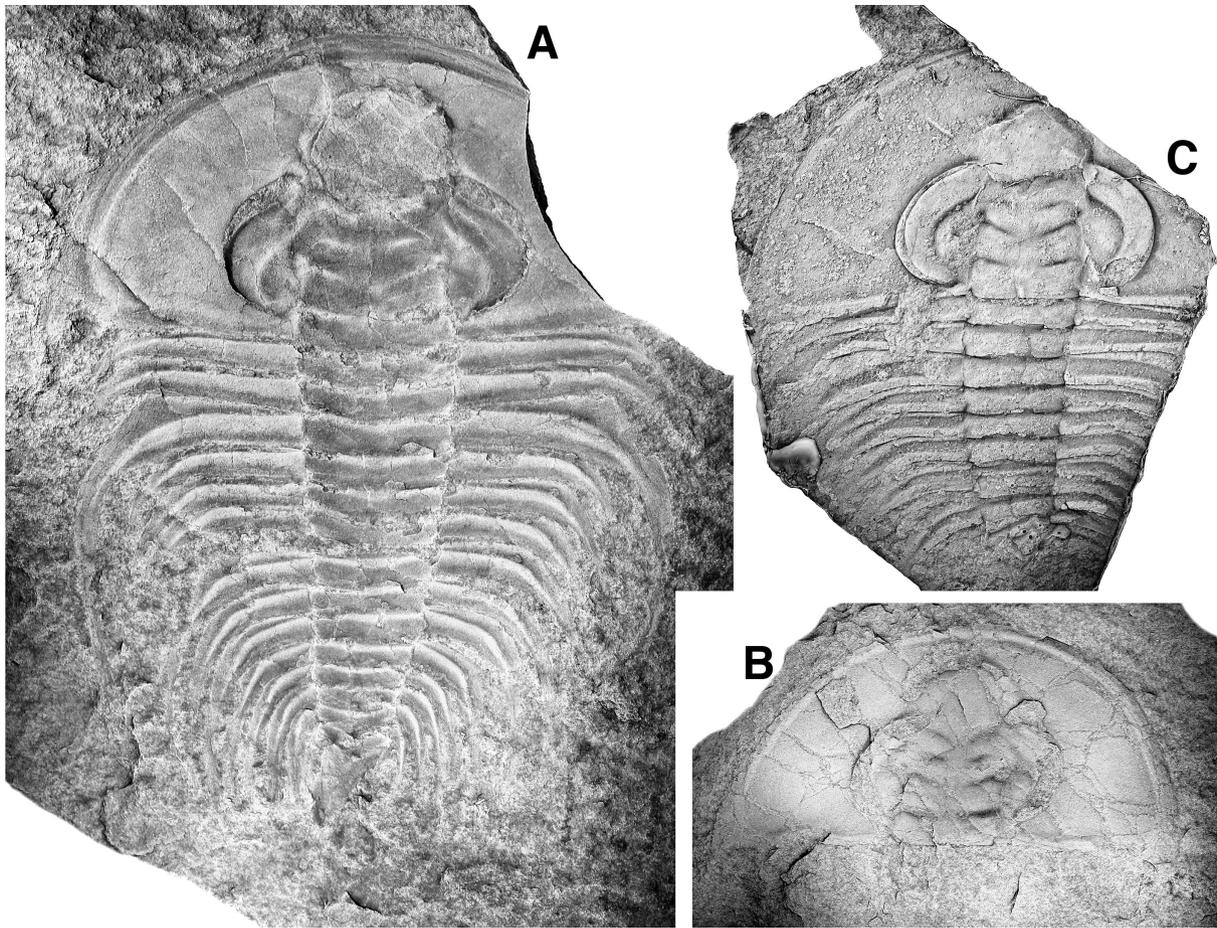


Figure 11. *Olenellus agellus* from the Parker Formation. **A**, cephalon, prothorax, and first opisthothoracic segment, external mould, FMNH UC12981, x1.5. **B**, cephalon, internal mould, FMNH 14675 P42, x0.75. **C**, tentatively assigned cephalon and incomplete prothorax, latex peel of external mould, MCZ 193183, x1.5. All in dorsal view. A, B from unknown locality near Georgia, Vermont. C from Locality 4789, Franklin County, Vermont.

distinction (if any) between *O. transitans*, *O. aff. transitans* and *O. puertoblancoensis*. Pending conclusion of that investigation, *O. aff. transitans* is conservatively left in open nomenclature.

Olenellus agellus Resser & Howell 1938 (Fig. 11)

- 1886 *Olenellus thompsoni* (Hall); Walcott (part), pl. 22, fig. 1, pl. 23, fig. 1 only.
 1889 *Olenellus thompsoni* (Hall); Lesley (part), text-fig. on p. 491 labelled pl. 22 only.
 1890b *Olenellus thompsoni* (Hall); Walcott (part), pl. 82, fig. 1, pl. 83, fig. 1 only.
 1897 *Olenellus thompsoni* (Hall); Frech, pl. 1a, fig. 7.
 1901 *Olenellus thompsoni* (Hall); Lindström, p. 12.
 1910 *Olenellus thompsoni* (Hall); Grabau & Shimer (part), p. 263, fig. 1555a only.
 1910 *Olenellus thompsoni* (Hall); Walcott (part), pl. 35, fig. 1 only.
 1919 *Olenellus thompsoni* (Hall); Bassler, p. 339, pl. 24.
 1938 *Olenellus agellus*; Resser & Howell (part), p. 223, pl. 9, figs 12, 13 only [not pl. 9, fig. 11 = *Olenellus transitans*].
 1999 *Olenellus agellus* Resser & Howell; Lieberman, p. 13, 15 [reference to MCZ 2482], 17, table 2, figs 1 [cladogram], 2.3, 2.4, 2.5.
 1999 *Olenellus agellus* Resser & Howell; Smith &

Lieberman, table 1.

2002 *Olenellus agellus* Resser & Howell; Lieberman, fig. 2 [cladogram].

2003 *Olenellus agellus* Resser & Howell; Lieberman, table 1.

Holotype. USNM 90806 (identified as USNM 15418b by Walcott 1910, pl. 35, fig. 1). This number refers to a suite of two specimens that includes the holotype (with a label “235x” affixed to it) and the paratype (with a label “235y” affixed to it). These specimens will be henceforth referred to as USNM 90806.235x and USNM 90806.235y, respectively.

Other material. See Appendix 2. MCZ 2467 was listed as a specimen of *O. thompsoni* by Lieberman (1998, p. 70; 1999, p. 15). However, examination of this specimen revealed that a prelabellar field might have been present, and it is herein treated as *O. cf. agellus*. MCZ 2482 was stated to represent either *O. agellus* or *O. thompsoni* by Lieberman (1999, p. 15, 17), with poor preservation rendering a definitive identification impossible. However, a prelabellar field is present, and the specimen is herein tentatively assigned to *O. agellus*.

Some specimens have been assigned to *Olenellus agellus* in earlier reports but have never been figured and were not examined during this study. The assignment of

those specimens to *O. agellus* is therefore not confirmed. Other specimens have at one time or another been assigned to *O. agellus* by various authors, but our examination of specimens or scrutiny of illustrations indicate that they were either misassigned or cannot be identified to species level. See Appendix 2 for details.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25, within the Parker Formation. Locality 4789, Franklin County: within the Parker Formation. Several specimens in museum collections are simply labelled as being collected from “Georgia, Vermont” or bear no locality information at all. The lithology of the slabs is consistent with these specimens having been collected from the Parker Formation.

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin directed more or less transversely or weakly posteriorly by up to 11°, distal portion flexed anteriorly by approximately 16–32° relative to proximal portion at intergenal angle located approximately 76–83% of distance from axial furrow to base of genal spine. Greatest observed cephalic length approximately 61 mm (sag.; MCZ 2469). Genal spine slender, base transversely opposite lateral margins of LO (more posteriorly on tentatively assigned specimen; Fig. 11C); length approximately half that of cephalon (sag.; USNM 90806.235y). Distance (tr.) between genal spine bases approximately 162–205% (average 189%) cephalic length (sag.). Short, pointed, intergenal spine on posterior cephalic border immediately distal to intergenal angle on at least some specimens (Fig. 11A–C); length approximately half that (exsag.) of LO or shorter. Cephalic border flattened, well defined around entire cephalon by distinct border furrow; width of anterior border opposite junction of ocular lobes with LA approximately 7–11% length (exsag.) of glabella. Preglabellar field well developed, sagittal length approximately once to twice width of anterior cephalic border (perhaps more than twice width of anterior border on tentatively assigned specimen; Fig. 11C). Plectrum present, often faint. Glabella weakly constricted at S1; approximately 82–87% cephalic length (sag.). Maximum width of LA approximately 100–116% (average 107%) basal glabellar width (tr.). Posterior margin of glabella more or less transverse or very weakly convex posteriorly. SO deep only abaxially, directed weakly posteriorly inwards. LO rectangular to subtrapezoidal, slightly narrowing anteriorly, length (exsag.) 13–17% that of glabella (sag.). S1 deepest abaxially, directed slightly more strongly posteriorly inwards than SO. L1 subtrapezoidal, narrows anteriorly; length (exsag.) 14–19% that of glabella (sag.). Lateral margins of LO and L1 bow slightly outward. S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, directed weakly posteriorly inwards. L2 widens anteriorly; anterolateral portion confluent with posterolateral portion of L3. S3 deepest midway between sagittal line and axial furrow, isolated from axial furrow, oriented anterolaterally away from axis until contact with ocular lobes. L3 broadly ‘M’-shaped; axial furrow slightly shallows at distal tips of L3. LA subovate in outline, approximately 63–93% (average 78%) as long (sag.) as wide (tr.), approximately 44–52% glabellar length (sag.), separated from extraocular area by a sharp break in slope, weakly convex and not prominently inflated relative to extraocular area (although precise convexity and degree of inflation is uncertain due to compaction); widest

at contact with anterior margin of ocular lobes. Tiny axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at 5–11°, crescentic, flat-topped; posterior tip transversely opposite midpoint or anterior half of lateral margin of LO. Shallow ocular furrow; deepest anteriorly, inner band slightly wider (tr.) than outer band. Interocular area weakly arched in transverse profile on at least some specimens (Fig. 11A, B) but appears flat-topped on others, approximately 78–126% (average 105%) as wide (tr.) as ocular lobes and 31–42% (average 35%) as wide (tr.) as extraocular area opposite S1. Posterior ocular line and weak extraocular genal caeca on some specimens (Fig. 11A, B). Terrace lines on anterior cephalic border (Fig. 11A) and doublure (Fig. 11B; MCZ 1793, YPM 72905). Tentatively assigned specimen bears Bertillon markings on axis of LO (Fig. 11C). Rostral plate and hypostome unknown.

Prothorax of 14 segments; axis approximately 87–103% as wide (tr.) as inner pleural region on T1, gently tapering posteriorly. Small axial node or spinule consistently present on posterior prothoracic segments from at least T8 or T9 to T14, increasing in size posteriorly from small nodes to axial spinelets (Fig. 11A; MCZ 1793; USNM 90806.235y); axial node or spinelet present on (T1? and) T2 of tentatively assigned specimen (Fig. 11C); axial structure apparently absent on T3–T7. Inner pleural regions of T1 and T2 transverse, slightly tapered distally, with straight margins; pleural spines of T1 and T2 divergent, sentate to weakly falcate, pleural spine of T2 slightly longer than that of T1. T3 weakly macropleural; pleural spine dolichospinous with posterior tip located approximately opposite end of prothorax (Fig. 11A; USNM 90806.235x). Inner pleural region of T4 transverse, slightly tapered distally, with slightly curved anterior margin to accommodate distal expansion of T3; inner pleural regions of T5–T9 transverse, parallel-sided, with straight margins; those of more posterior prothoracic segments increasingly divergent to subpendent, with increasingly curved margins. Pleural spines of T4 slender, divergent, weakly falcate; those of T5–T14 falcate, progressively increasing in length down the prothorax, transitioning from divergent to subpendent on T9–T14. Pleural furrows of all prothoracic segments wide (exsag.), occupying much of inner pleural region, anterior wall steeper than posterior wall; extending onto pleural spines of all prothoracic segments. Lirae or terrace lines on pleural spines of at least T1–T3, T5, T6 and T8 on some specimens (MCZ 1793, USNM 90806.235x). Long axial spine on T15 (total length unknown), base as wide as T15 axis. Rest of opisthothorax and pygidium unknown.

Remarks. The taxonomic history of *Olenellus agellus* is rather convoluted. Resser & Howell (1938, p. 223) differentiated their new species *O. agellus* from *O. thompsoni* based on the presence of a preglabellar field, proportionally longer ocular lobes and a proportionally wider cephalic border in the former. However, the inadequacy of early illustrations mean that authors have disagreed over the interpretation of the presence or absence of a preglabellar field on particular specimens. Walcott’s original sketches of USNM 90806.235x and USNM 90806.235y (Walcott 1886, pl. 23, fig. 1, pl. 22, fig. 1, respectively) showed a clear preglabellar field on each specimen, in keeping with the diagnosis of *O. agellus* provided by Resser & Howell (1938). However, Walcott (1910, pl. 35, fig. 1) had subsequently amended his earlier illustration of USNM 90806.235x (later to be designated the holotype of *O.*

agellus) so that a preglabellar field was absent. He noted in the accompanying caption (Walcott 1910, p. 404) that the preglabellar field shown in the earlier sketch was an error on the part of the draftsman, and that the same was true of his earlier sketch of USNM 90806.235y. Shaw (1955, p. 793) synonymised *O. agellus* with *O. thompsoni* based on his observation that the MCZ collections contained a full gradation of morphologies from typical *O. thompsoni* (lacking a preglabellar field) to typical *O. agellus* (with a preglabellar field). Recent typographical errors have only added to the confusion: for example, Lieberman (1999) included the holotype and one paratype of *O. agellus* figured by Resser & Howell (1938, pl. 9, figs 12, 13) under the synonymy of both *O. thompsoni* (p. 15) and *O. agellus* (p. 17), and the third specimen figured as *O. agellus* by Resser & Howell (1938, pl. 9, fig. 11; USNM 14675.236a) under the synonymy of both *O. transitans* (p. 15) and *O. agellus* (p. 17). Examination of these specimens during the present study confirms that all possess a preglabellar field but that only USNM 90806.235x and USNM 90806.235y can be assigned to *O. agellus*; USNM 14675.236a is *O. transitans*.

The present study demonstrates that *Olenellus agellus* differs from *O. thompsoni* most obviously in possessing a preglabellar field—this is absent in *O. thompsoni* (and is consistent with Resser & Howell 1938; Lieberman 1999, Olenellinae analysis, character 3). The pleural spine on T3 is also markedly proportionally longer on *O. agellus* than on *O. thompsoni* (Lieberman 1999, Olenellinae analysis, character 12). Lieberman (1999, Olenellinae analysis, character 2) also correctly coded a plectrum as being present on *O. agellus* and absent on *O. thompsoni*, although presence of a plectrum is conditional upon possession of a preglabellar field.

The differentiation of *Olenellus agellus* from *O. transitans* is far more subtle. Both bear a preglabellar field and a plectrum, and their thoracic morphologies are indistinguishable. Lieberman (1999, Olenellinae analysis) coded state differences between the species in several characters, but none of these are unambiguously supported in this study. Two putative differences relate to differences only in the degree of variation expressed by traits (i.e., the size of the preglabellar field [character 3] and the depth of S1 across the sagittal line [character 7]); one almost certainly relates to ontogenetic allometry (i.e., the orientation of the anterior margin of T3 [character 11]); one is ambiguous given that all known material of both species has experienced compactional deformation (i.e., the dorsal convexity of the extraocular area [character 10]); two were miscoded (e.g., the width of LA relative to that of LO in *O. transitans* [character 4] and the ratio of the width of T7 relative to the width of T3 [character 13]); and two were simply not evident to the present authors (e.g., the profile of the anterior cephalic border [character 1] and the condition of a furrow across the ocular lobe [character 8]).

This study finds that the species consistently differ only in terms of the form of LA: this structure is proportionally wider (tr., relative to its sagittal length) in *Olenellus agellus* relative to *O. transitans* (two-sample t-test of LA length:width ratio between the species, $t = 5.7914$, $p < 0.0001$). Associated with this difference in proportional width, the outline of LA across the sagittal line is more broadly rounded in *O. agellus* but is more acuminate in *O. transitans*. The extraocular area also tends to be proportionally wider (tr.) relative to sagittal glabella length

in *O. agellus* than in *O. transitans*, but this difference is not significant at 95% confidence (analyses not presented).

***Olenellus crassimarginatus* Walcott 1910 (Fig. 12)**

- 1886 *Olenellus thompsoni* (Hall); Walcott (part), pl. 17, fig. 1 only.
 1890b *Olenellus thompsoni* (Hall); Walcott (part), pl. 83, fig. 1b only.
 1910 *Olenellus thompsoni crassimarginatus*; Walcott (part), p. 340, 341, pl. 35, figs 8, 10 only [not pl. 35, fig. 9 = *Olenellus* sp. indet.].
 1912a *Olenellus thompsoni crassimarginatus* Walcott; Walcott, p. 188, 201?
 ?1912a *Olenellus thompsoni rudis*; Walcott, p. 172.
 1936 *Olenellus thompsoni* var. *crassimarginatus* Walcott; Grabau, p. 27.
 1936 *Olenellus thompsoni crassimarginatus* Walcott; Grabau, p. 124.
 ?1936 *Olenellus thompsoni rudis* Walcott; Grabau, p. 124.
 1937 *Olenellus thompsoni* var. *crassimarginatus* Walcott; Schuchert, p. 1026.
 1938 *Olenellus crassimarginatus* Walcott; Resser & Howell, p. 224, pl. 7, fig. 2.
 1938 *Olenellus latilimbatus*; Resser & Howell, p. 222, pl. 6, fig. 9.
 1938 *Olenellus wanneri*; Resser & Howell, p. 224, pl. 7, fig. 1.
 1948 *Olenellus crassimarginatus* Walcott; Kindle & Tasch, p. 137.
 1948 *Olenellus wanneri* Resser & Howell; Kindle & Tasch, p. 137.
 1956 *Olenellus crassimarginatus* Walcott; Harrington, p. 58.
 1956 *Olenellus wanneri* Resser & Howell; Harrington, p. 58.
 1956 *Olenellus thompsoni crassimarginatus* Walcott; Lochman, p. 1354.
 1960 *Olenellus crassimarginatus* Walcott; Kielan, p. 87.
 1960 *Olenellus latilimbatus* Resser & Howell; Kielan, p. 87.
 1960 *Olenellus wanneri* Resser & Howell; Kielan, p. 87.
 1998 *Olenellus crassimarginatus* Walcott; Lieberman, p. 68.
 1999 *Olenellus crassimarginatus* Walcott; Lieberman, p. 13, 25, 26, fig. 1 [cladogram], table 2.
 1999 *Olenellus crassimarginatus* Walcott; Smith & Lieberman, table 1.
 2002 *Olenellus crassimarginatus* Walcott; Lieberman, fig. 2 [cladogram].
 2003 *Olenellus crassimarginatus* Walcott; Lieberman, table 1.
 2005 *Olenellus?* *crassimarginatus* Walcott; Skinner, p. 172, 179, 180, fig. 14a, b.

Holotype. USNM 90810 (formerly USNM 56836a), from USNM Locality 25 (Fig. 12A).

Other material. The following description is based on examination of the holotype plus USNM 56837b (Fig. 12B; from USNM Locality 8q; also figured by Walcott 1910, pl. 35, fig. 10; Resser & Howell 1938, pl. 7, fig. 1, as holotype of *Olenellus wanneri* Resser & Howell 1938), and USNM 90811 (Fig. 12C; from USNM Locality 22L; figured by Resser & Howell 1938, pl. 6, fig. 9, as holotype of *O. latilimbatus* Resser & Howell 1938).

Resser & Howell (1938, p. 224) stated that USNM

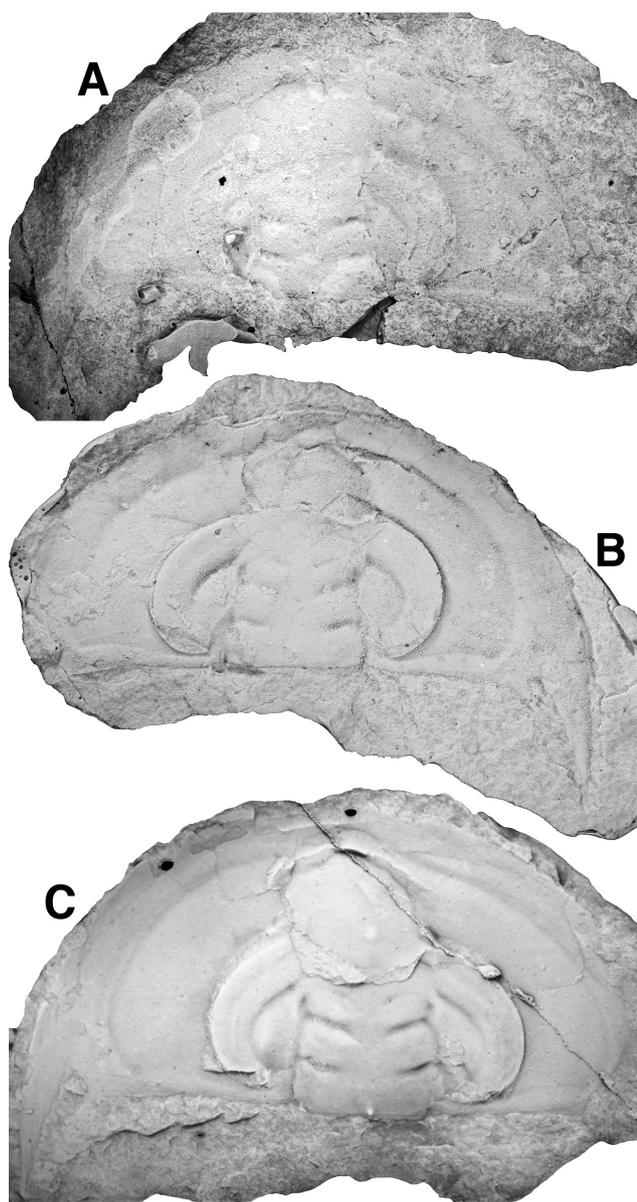


Figure 12. Cephalons of *Olenellus crassimarginatus*. **A**, latex replica of internal mould, USNM 90810 (holotype), x2. **B**, latex replica, USNM 56837b (former holotype of *Olenellus wanneri*), x1.3. **C**, latex replica, USNM 90811 (former holotype of *Olenellus latilimbatus*), x1. All in dorsal view. **A** from Parker Formation at Parker quarry, Franklin County, Vermont. **B** from Emigsville Member of Kinzers Formation at USNM Locality 8q, York County, Pennsylvania. **C** from Emigsville Member of Kinzers Formation at USNM Locality 22L, Getz quarry, Lancaster County, Pennsylvania.

56837 contains the holotype and paratypes of *Olenellus wanneri*, but only the holotype was examined during the present study. Walcott (1910) assigned another cephalon from USNM Locality 8q to *O. crassimarginatus* (USNM 56837a), but the illustration of this specimen (Walcott 1910, pl. 35, fig. 9) indicates that this identification is erroneous.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25, in the Parker Formation. Pennsylvania: York, York County: USNM Locality 8q, Emigsville Member of Kinzers Formation (see Walcott 1910, p. 341; type locality for *Olenellus wanneri*; see Resser & Howell

1938, p. 224). Getz quarry, Lancaster County: USNM Locality 22L, Emigsville Member of Kinzers Formation (type locality of *O. latilimbatus*; see Resser & Howell 1938, p. 222).

Resser & Howell (1938, p. 224) also reported *Olenellus wanneri* from USNM Locality 12w, but no material was illustrated. Walcott (1910, p. 341; 1912a, p. 201) also reported this species from USNM Locality 49 and USNM Locality 49a, but both of these Pennsylvania occurrences were disputed by Resser & Howell (1938, p. 224). Until examination of the material from these three localities can be undertaken, these purported occurrences of *O. crassimarginatus* cannot be substantiated.

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin directed weakly posteriorly by up to 8° from transverse, distal portion flexed anteriorly by approximately 7–42° relative to proximal portion at intergenal angle located approximately 80% of distance from axial furrow to base of genal spine. Greatest observed cephalic length estimated to exceed 31 mm (sag.; Fig. 12C). Genal spine fairly slender, broad-based; base transversely opposite posterior portion of lateral margins of LO; length approximately half that of cephalon (sag.). Distance (tr.) between genal spine bases approximately 175–190% of cephalic length (sag.). Prominent intergenal spine projects posterolaterally from posterior cephalic margin; base of inner margin of spine located at intergenal angle; width (tr.) of base of intergenal spine approximately equal to distance along distal portion of posterior cephalic margin between outer margin of intergenal spine base and inner margin of genal spine base; length of intergenal spine almost equal to length (exsag.) of LO. Cephalic border flattened, well defined around entire cephalon by distinct border furrow; width of anterior border opposite junction of ocular lobes with LA approximately 17–19% length (sag.) of glabella; widening near base of genal spines; progressively tapering proximally along posterior cephalic margin so that at axial furrow width of border is approximately one-third length (exsag.) of LO. Preglabellar field absent. Glabella weakly constricted at S1; approximately 85% of cephalic length (sag.). Maximum width of LA approximately equal to basal glabellar width (tr.). Posterior margin of glabella more or less transverse. SO deep only abaxially, directed weakly posteriorly inwards. LO subrectangular to subtrapezoidal, slightly narrowing anteriorly, length (exsag.) 16–18% that of glabella (sag.). S1 deepest abaxially, approximately parallel to SO. L1 subtrapezoidal, slightly narrowing anteriorly; length (exsag.) 13–17% that of glabella (sag.). Lateral margins of LO and L1 bow slightly outward. S2 and particularly S3 shallower than SO and S1. S2 more or less transversely directed, convex anteriorly either side of axis, deepest midway between sagittal line and axial furrow, extremely shallow connection to axial furrow. L2 very slightly widens anteriorly. S3 strongly convex anteriorly either side of axis, arcs anterolaterally away from axis until contact with ocular lobes, deepest midway between sagittal line and axial furrow, extremely shallow connection to axial furrow. L3 broadly 'M'-shaped, becoming shorter (exsag.) distally; lateral margins extend slightly beyond those of L2; distal tips of L3 poorly defined by very shallow axial furrow so that they are almost confluent with anteriormost interocular area. LA subcircular in outline, approximately 66–85% as long (sag.) as wide (tr.) and approximately 43–48% of glabellar length (sag.), weakly convex and not

prominently inflated relative to extraocular area (although precise convexity and degree of inflation is uncertain due to compaction); widest at contact with anterior margin of ocular lobes. Tiny axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at approximately 13–20°, crescentic, flat-topped; posterior tip transversely opposite posterior half of lateral margin of LO. Ocular furrow very shallow, deepest anteriorly, width (tr.) of inner band approximately equal to that of outer band. Interocular area slightly arched in transverse section (Fig. 12A; less so on more strongly compacted specimens), approximately as wide (tr.) as ocular lobes and about 41–57% as wide (tr.) as extraocular area opposite S1. Genal ridge present on at least one specimen (Fig. 12B). Rostral plate, hypostome, thorax and pygidium unknown.

Remarks. Walcott (1910, pl. 35, figs 8, 10) included specimens from the Parker Formation of Vermont and the Kinzers Formation of Pennsylvania in his original description of *Olenellus crassimarginatus*. Resser & Howell (1938) subsequently restricted *O. crassimarginatus* to the holotype from Vermont, and assigned the Pennsylvanian material to two new species, *O. latilimbatus* (Fig. 12C) and *O. wanneri* (Fig. 12B). According to Resser & Howell (1938, p. 224), *O. wanneri* differs from *O. crassimarginatus* in having “more circular eye lobes, more deeply impressed furrows, stronger intergenal spines, narrower cheeks, and possibly a different surface ornamentation. In addition, the rim is less even in width, increasing toward the genal angles”. Resser & Howell (1938, p. 222) compared *O. latilimbatus* to *O. rodnyi*, but provided no justification for the distinction of *O. latilimbatus* from either *O. crassimarginatus* or *O. wanneri*. Lieberman (1999, p. 26) considered *O. latilimbatus* and *O. wanneri* to be junior subjective synonyms of *O. crassimarginatus*. The type material of all three named species was examined during the course of the present study, and Lieberman’s (1999) conclusion is supported.

All specimens examined during this study have experienced compactional deformation, which complicates interpretation of some aspects of their morphology. Most obviously, the original convexity of the cephalon cannot be unambiguously determined (although Lieberman [1999, Olenellinae analysis, character 10] coded *Olenellus crassimarginatus* as having a gently convex extraocular area). The form of LA has also been affected by compaction: on the holotype the maximum width (tr.) of LA is approximately equal to the basal glabellar width (Fig. 12A), whereas, on the heavily fractured specimen USNM 56837b, the maximum width (tr.) of LA is less than the basal glabellar width (Fig. 12B; as reflected in the coding by Lieberman 1999, Olenellinae analysis, character 4).

Olenellus crassimarginatus differs most obviously from all other species of *Olenellus* by its proportionally broad cephalic border. This feature is shared with species of *Laudonia* Harrington 1956, *Lochmanolenellus* Lieberman 1998 (e.g., Webster & Bohach 2014) and *Fremontella* Harrington 1956 (e.g., Walcott 1910, pl. 31, figs 1, 3; Harrington 1956, pl. 15, fig. 1; Palmer & Repina in Whittington *et al.* 1997, fig. 256.2; Peel 2011, fig. 2f, h). *Olenellus crassimarginatus* differs markedly from *Laudonia* and *Lochmanolenellus* in other traits (see the diagnoses of Webster & Bohach 2014), and the fact that these taxa all share a broad cephalic border is likely to reflect homoplasy. *Olenellus crassimarginatus* and species

of *Fremontella* share not only a broad cephalic border, but also many details of glabellar morphology—indeed, a strong similarity between *O. crassimarginatus* and *F. halli* (Walcott, 1910) “in the glabellar features, attachment of the eye lobe to frontal glabellar lobe, and wide, flat cephalic border” was noted by Harrington (1956, p. 58) when he named *Fremontella*. The primary differences between *O. crassimarginatus* and *Fremontella* species are in the degree of anterior advancement of the genal spine bases (far more anteriorly placed in *Fremontella* species), the length of the ocular lobes (relatively shorter in *Fremontella* species), and the presence (in *O. crassimarginatus*) versus absence (*Fremontella* species) of an intergenal spine at morphological maturity. Cephalic outline and ocular lobe length are known to vary greatly among closely related species within other olenelloid genera (e.g., Webster 2007b; Webster & Bohach 2014). Future work will assess the phylogenetic relationship between *O. crassimarginatus* and species of *Fremontella*.

Olenellus aff. fowleri Palmer 1998b (Fig. 13)

1938 *Olenellus georgiensis*; Resser & Howell (part), p. 220, pl. 5, fig. 6 only [not pl. 5, fig. 7 = *Mesonacis vermontanus*].

1952 *Olenellus georgiensis* Resser & Howell; Hupé, p. 122.

1953 *Olenellus georgiensis* Resser & Howell; Hupé, p. 128.

1957 *Olenellus georgiensis* Resser & Howell; Raw, p. 149, 150.

1999 *Olenellus thompsoni* (Hall); Lieberman (part), p. 41 [reference to Resser & Howell 1938, pl. 5, fig. 6 = USNM 90797 only].

Material. Known from two specimens, USNM 90797 (Fig. 13A; also figured by Resser & Howell 1938, pl. 5, fig. 6) and FMNH PE58499 (Fig. 13B), approximately 13 mm and 14 mm in sagittal cephalic length, respectively.

Occurrence. Vermont: Parker quarry, Franklin County: USNM Locality 25 or the effectively equivalent USNM Locality 319m, in the Parker Formation. Powerline section, Chittenden County: ICS-10508, in the middle Monkton Formation.

Description. Cephalon semicircular in outline; proximal portion of posterior cephalic margin directed weakly posteriorly by up to 6° from the transverse, distal portion flexed anteriorly by approximately 33° relative to proximal portion at or near base of intergenal spine located approximately 94% of distance from axial furrow to base of genal spine. Greatest observed cephalic length approximately 14 mm (sag.; Fig. 13B). Genal spine slender, base transversely opposite posterior margin of LO; length approximately two-fifths as long as cephalon (sag.). Distance (tr.) between genal spine bases approximately 218–257% of cephalic length (sag.). Short, pointed intergenal spine on posterior cephalic border at or near point of anterior flexure of posterior cephalic margin and close to base of genal spine (Fig. 13A). Cephalic border well defined around entire cephalon by distinct border furrow; from summit, anterior border slopes steeply outwards to cephalic margin and less steeply inwards to border furrow; relief of lateral cephalic border is more subdued near base of genal spine; width of anterior border opposite junction of ocular lobes with LA approximately 8–10% glabellar length (exsag.). Preglabellar field short, sagittal length slightly less than that of anterior cephalic border. Plectrum

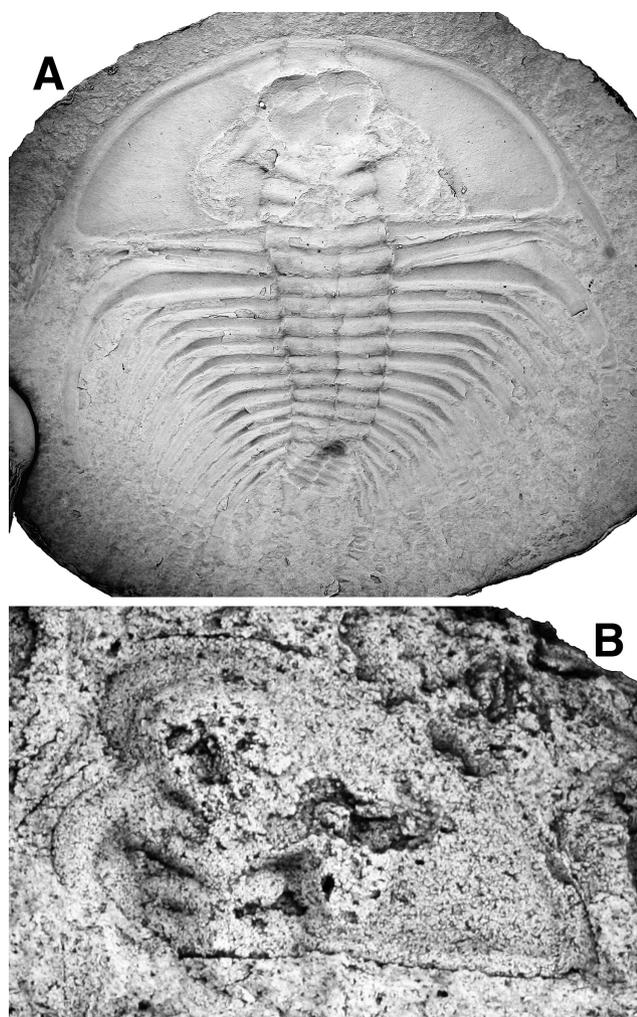


Figure 13. *Olenellus* aff. *fowleri*. **A**, almost complete dorsal exoskeleton and impression of hypostome, latex peel of external mould, USNM 90797, x2. **B**, cephalon, internal mould, FMNH PE58499, x3. Both in dorsal view. A from Parker Formation at Parker quarry, Franklin County, Vermont. B from Monkton Formation at ICS-10508, Powerline section, Chittenden County, Vermont.

either very weakly developed or absent (condition unclear due to poor preservation). Glabella weakly constricted at S1; approximately 83–87% of cephalic length (sag.). LA slightly wider than basal glabellar width (tr.). Posterior margin of glabella more or less transverse (Fig. 13B). SO deep only abaxially, directed weakly posteriorly inwards. LO subtrapezoidal, slightly narrowing anteriorly. S1 deepest abaxially, approximately parallel to SO. L1 subtrapezoidal, slightly narrowing anteriorly; length (exsag.) approximately 17% that of glabella (sag.). S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, directed weakly posteriorly inwards. L2 and L3 confluent distally, widen (tr.) anteriorly until contact with ocular lobes. S3 deepest midway between sagittal line and axial furrow, isolated from axial furrow, directed anterolaterally away from axis until contact with ocular lobes. LA subcircular in outline, approximately half of glabellar length (sag.), separated from extraocular area by a sharp break in slope, convex and not prominently inflated relative to extraocular area; widest at contact with anterior margin of ocular lobes. Prominent axial node on posterior margin of LO.

Presence or absence of any axial structure on L3 and LA cannot be determined on available specimens. Ocular lobes crescentic, flat-topped; posterior tip transversely opposite approximately midlength of lateral margin of LO. Shallow ocular furrow deepest anteriorly, inner band slightly wider (tr.) than outer band. Interocular area slopes down from ocular lobes to axial furrow, approximately as wide (tr.) as ocular lobes and approximately 35–40% as wide (tr.) as extraocular area opposite S1. Extraocular genal caeca and genal ridge weakly developed (Fig. 13A); presence or absence of intergenal ridge and posterior ocular line cannot be determined on available specimens. Terrace lines on cephalic doublure and ventral surface of genal spines (Fig. 13A). Hypostome preserved in place on USNM 90797 (Fig. 13A), but too poorly preserved for description.

Prothorax of 14 segments; width (tr.) of axis approximately 75% that (tr.) of inner pleural region on T1, slightly tapering posteriorly. Axial node not evident on T1 to at least T10 (although interpretation is hindered by incomplete preservation and taphonomic fracturing); condition of any axial nodes on more posterior segments unclear due to obstruction by opisthothorax. Inner pleural regions of T1 and T2 transverse, slightly tapering distally, with straight margins; pleural spines of T1 and T2 divergent and sentate to weakly falcate, pleural spine of T2 slightly longer than that of T1. T3 macropleural, with anterior margin directed anterolaterally at approximately 8° to transverse; pleural spine macrospinous with posterior tip located approximately transversely opposite end of prothorax. Inner pleural region of T4 transverse, very slightly tapering distally to accommodate distal expansion of T3; inner pleural regions of T5–T9 transverse, parallel-sided, with straight margins; those of more posterior prothoracic segments increasingly divergent, with increasingly curved margins. Pleural spines of T4–T14 divergent, falcate; distal tip of T4 pleural spine located transversely opposite axis of T8, pleural spines of more posterior segments progressively increasing in length down the prothorax. Pleural furrows of all prothoracic segments wide (exsag.), occupying much of inner pleural region, anterior wall steeper than posterior wall; extending onto pleural spines of all segments.

Opisthothorax poorly preserved; consisting of at least four segments. Long axial spine on T15 (full length unknown), base apparently as wide as T15 axis; presence or absence of axial structures on more posterior segments cannot be determined. Inner pleural regions apparently well developed, relatively wide (tr.), although distal portions not clearly preserved; condition of pleural spines unclear. Shallow pleural furrows evident at least adaxially. Poorly preserved structure posterior to T18 might represent incomplete pygidium or fragments of one or more additional opisthothoracic segments.

Remarks. Resser & Howell (1938, pl. 5, fig. 6) considered the articulated specimen from the Parker quarry (Fig. 13A) to be a paratype of *Olenellus georgiensis*. This species, including the paratype, was synonymised with *Mesonacis vermontanus* by Shaw (1955, p. 794). Lieberman (1999, p. 41) agreed that the holotype of *O. georgiensis* represented *M. vermontanus*, but reassigned the paratype specimen to *O. thompsoni*.

However, the paratype specimen differs from *Olenellus thompsoni* in several features: (1) the extraocular area is proportionally wider (tr.) on USNM 90797 than on similarly sized specimens of *O. thompsoni*; (2) the ocular

lobes of USNM 90797 are proportionally slightly longer (the posterior tips being located transversely opposite the midlength rather than the anterior third of the lateral margins of LO); (3) USNM 90797 bears a short preglabellar field; (4) the anterior margin of T3 is directed slightly more strongly anteriorly on USNM 90797 than in *O. thompsoni* and, probably related to this, the anterior margin of the inner part of the pleural furrow on T3 is directed more transversely on USNM 90797 but is directed posterolaterally in *O. thompsoni*; (5) the pleural spines of T3 extend approximately the entire length of the rest of the prothorax on USNM 90797, but not beyond T10 in *O. thompsoni*; and (6) the pleural spines of T4 and all more posterior prothoracic segments are markedly longer on USNM 90797 than on *O. thompsoni*.

The differences between USNM 90797 and *Olenellus thompsoni* in ocular lobe length and in the condition of a preglabellar field could be attributable to difference in size, because proportional shortening of the ocular lobes and decrease in size (and ultimate loss) of a preglabellar field are ontogenetic trends that have been documented in other olenellids (e.g., *O. gilberti*; Webster 2015). The fourth difference listed above, relating to differences in orientation of the anterior margin of the inner pleural region and inner part of the pleural furrow of T3, could conceivably result from compaction-related rotation of the pleural fields, although supporting evidence for this (e.g., exoskeletal fractures, or similar displacement of surrounding pleurae) is scant. However, the differences in width of the extraocular area and in the lengths of prothoracic pleural spines (including T3) preclude assignment of USNM 90797 to *O. thompsoni*. By comparison to patterns seen in other olenelloids, differences of such magnitude are not defensibly attributable to ontogenetic allometry or intraspecific variation.

Instead, the proportionally wide extraocular area, the proportionally long ocular lobes, and the prothoracic morphology all suggest a close affinity of USNM 90797 to *Olenellus fowleri* Palmer 1998b. Differences between USNM 90797 and *O. fowleri* preclude their conspecificity. For example, *O. fowleri* bears a proportionally narrower (tr.) glabella, a slightly longer preglabellar field, a more prominent plectrum, and axial nodes on all prothoracic segments. Additionally, the most deeply incised portion of S2 in USNM 90797 is longer while in *O. fowleri* it is more dimple-like. Furthermore, *O. fowleri* bears a distinctive granular ornament that is not evident on USNM 90797. The opisthothorax of USNM 90797 is too poorly preserved for detailed comparison with *O. fowleri*, but if the structure behind T18 on USNM 90797 is a pygidium then the opisthothorax of that specimen consists of many fewer segments than *O. fowleri*.

On account of these differences, and being unwilling to formally name a new species based on such limited material, USNM 90797 (and a seemingly conspecific specimen from the Monkton Formation; Fig. 13B) are herein treated as *Olenellus* aff. *fowleri*. A similar Cordilleran form from the *Bolbolenellus euryparia* Zone has also been referred to as *O. aff. fowleri* (Webster 2011a, b). Ongoing work will determine whether the Cordilleran and the Vermont forms are either conspecific or represent a species complex.

The configuration of the sclerites on USNM 90797 (Fig. 13A) is worthy of mention. The leading edge of the prothorax is telescoped anteriorly below the posterior margin of the cephalon, and the opisthothorax is flipped

as if the specimen was enrolled, with the flexure being accommodated at the T14–T15 articulation. Given the pattern of olenelloid molting behaviour proposed by Webster (2015, p. 68), such an arrangement is consistent with this specimen representing an exuvium. However, interpretation of USNM 90797 as an exuvium as opposed to a biostratinomically modified carcass must remain ambiguous because the hypostome is preserved more or less in place (see discussion by Webster 2015, p. 68).

***Olenellus* sp. indet.** (Fig 14A)

Material. FMNH PE58498.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10508, in the middle Monkton Formation.

Remarks. Attention is drawn to this very poorly preserved and incomplete cephalon because it appears to possess a preglabellar field and a moderately elongate LA. Such features are inconsistent with other species currently documented from the Monkton Formation, so this specimen adds to the diversity of olenellid species within that formation. The specimen resembles *Olenellus transitans* except that the interocular area slopes down inwards and S2 appears to be fairly shallowly incised relative to other glabellar furrows.

***Olenellus?* sp. indet.** (Fig 14B)

Material. FMNH PE58495.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10508, in the middle Monkton Formation.

Remarks. This single cephalon is poorly preserved and incomplete, but appears to represent an olenellid species otherwise unknown from the Monkton Formation. The interocular area is slightly arched and generally slopes down towards the axial furrow. S2 and S3 are clearly shallower than SO and S1. Interestingly, L2, L3 and LA are quite strongly vaulted and their summits are considerably higher than the dorsal surface of the ocular lobes. Such vaulting is not seen among other species of *Olenellus*, so this form is only tentatively referred to that genus.

Family BICERATOPSIDAE Pack & Gayle 1971

***Bolbolenellus* Palmer & Repina 1993**

Type species. *Olenellus euryparia* Palmer & Halley 1979.

***Bolbolenellus hermani* (Kindle & Tasch 1948)**

1948 *Olenellus hermani*; Kindle & Tasch, p. 134, 136, 137, pl. 1, figs 1–3.

1949 *Olenellus hermani* Kindle & Tasch; Tasch, p. 1.

1952 *Olenellus hermani* Kindle & Tasch; Tasch, p. 486, fig. 11.

1954 *Olenellus hermani* Kindle & Tasch; Shaw, p. 1044.

1955 *Olenellus hermani* Kindle & Tasch; Shaw, p. 792.

1956 *Olenellus hermani* Kindle & Tasch; Lochman, p. 1354.

1957b *Olenellus hermani* Kindle & Tasch; Shaw, p. 814.

1958 *Olenellus hermani* Kindle & Tasch; Öpik, p. 27.

1962 *Esmereldina* [sic] *hermani* (Kindle & Tasch); Shaw, p. 333, pl. 50, figs 30–33.

1972 *Olenellus hermani* Kindle & Tasch; Fritz, p. 13.

1973 “Genus undetermined”; Fritz, p. 13.

1991 *Olenellus hermani* Kindle & Tasch; Fritz, p. 15.

1992 *Olenellus hermani* Kindle & Tasch; Fritz, p. 20.

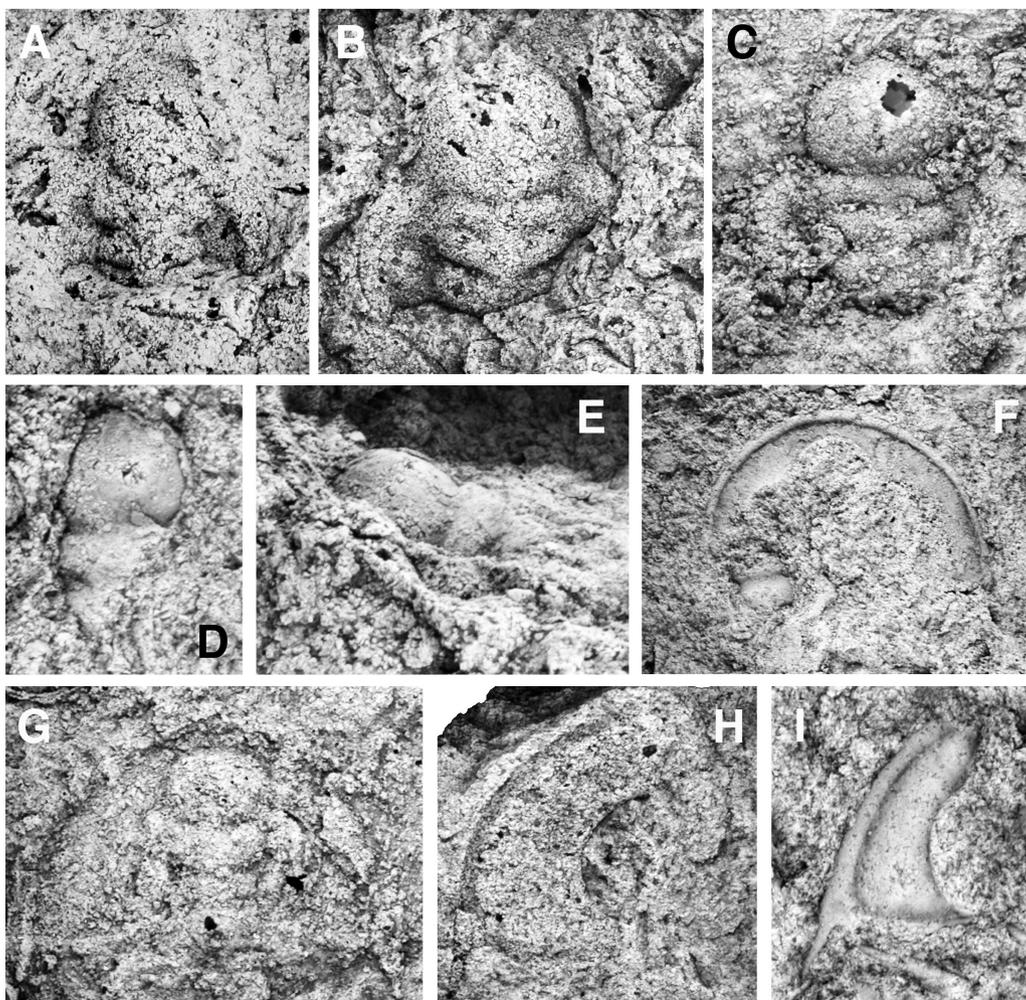


Figure 14. Various olenelloids from the Monkton Formation. **A**, *Olenellus* sp. indet., incomplete cephalon, internal mould, dorsal view, FMNH PE58498, x3. **B**, *Olenellus?* sp. indet., incomplete cephalon, internal mould, dorsal view, FMNH PE58495, x3. **C**, *Bolbolenellus* cf. *brevispinus*, incomplete cephalon, latex peel of external mould, dorsal view, FMNH PE58494, x3. **D, E**, *Bolbolenellus* sp. indet., incomplete cephalon, dorsal and oblique dorsolateral views, respectively, FMNH PE58493, x5. **F**, olenelloid sp. indet. A, incomplete cephalon, internal mould, dorsal view, NYSM 18379, x5. **G**, olenelloid sp. indet. B, incomplete cephalon, latex peel of external mould, dorsal view, FMNH PE58497, x3. **H**, olenelloid sp. indet. B?, tentatively assigned incomplete cephalon, internal mould, dorsal view, FMNH PE58492, x3. **I**, olenelloid sp. indet. C, fragmentary cephalon, dorsal view, FMNH PE58500, x4. A, B, G, I from ICS-10508, Powerline section, Chittenden County, Vermont. C–E, H from ICS-10507, Powerline section, Chittenden County, Vermont. F from Colchester, Chittenden County, Vermont.

1998b *Bolbolenellus hermani* (Kindle & Tasch); Palmer, p. 661, 663, 665.

1999 *Bolbolenellus hermani* (Kindle & Tasch); Lieberman (part), p. 134, 138, 139 [not reference to California specimen = *Bolbolenellus brevispinus*], table 19, fig. 21 [cladogram].

2002 *Bolbolenellus hermani* (Kindle & Tasch); Lieberman, fig. 2 [cladogram].

2003 *Bolbolenellus hermani* (Kindle & Tasch); Lieberman, table 1.

2005 *Bolbolenellus hermani* (Kindle & Tasch); Webster, p. 196.

Holotype. The holotype (Kindle & Tasch 1948, pl. 1, figs 1, 2; Shaw 1962, pl. 50, figs 31–33) was kept in the private collection of Cecil H. Kindle (Shaw 1955, 1962) and is apparently now lost (Lieberman 1999). Absence of additional specimens means that a neotype cannot be designated (see below). Fortunately, a plaster cast of the holotype exists in the biological collections of the USNM

(examined by MW).

Other material. The only other undisputed specimen of *Bolbolenellus hermani* is the paratype (Kindle & Tasch 1948, pl. 1, fig. 3; Shaw 1962, pl. 50, fig. 30), which was also kept in Kindle's private collection and cannot now be located. Lieberman (1999, p. 139) listed MCZ 5029 (subsequently renumbered as MCZ 113849) as an additional specimen of this species. MCZ 113849 is a multispecimen collection made by P. E. Raymond in 1942 from the "lower 10 feet of the Parker Slate, two miles west of Georgia Center, Vermont" (quoted from the museum label) and was examined during this study. The collection consists of seven pieces of poorly cemented, rusty-weathering sandstone with trilobite fragments. None of the fragments can be reliably identified to generic level, so specific assignment is impossible. The largest fragment is the anterior portion of LA and the anterior border of an olenelloid, but LA is not well inflated, and the anterior border is a ledge that is flattened rather than rounded in cross section; these are not

features typical of *B. hermani*. Another moderately large fragment shows an arched interocular area and ocular lobes that terminate approximately opposite LO. The rest of the collection contains one indeterminate thoracic pleura and four indeterminate cephalic fragments. The present investigation does not support Lieberman's (1999) recognition of *B. hermani* within this collection.

Occurrence. Vermont: Locality M-WC-1, Chittenden County: in the middle Monkton Formation (above; also Kindle & Tasch 1948).

Remarks. Both known specimens were poorly preserved internal moulds of incomplete cephalon in sandstone, that together provide information only on the anterior portion of the glabella, the anterior cephalic border, the ocular lobes, and the interocular area. *Bolbolonellus hermani* is very similar to the much better known Cordilleran species *B. brevispinus* Palmer 1998b—indeed, Palmer (1998b, p. 665) stated that “possible synonymy of the two species should be reexamined if better material is ever obtained for *B. hermani*”, and Lieberman (1999) considered the Appalachian and Cordilleran material to be conspecific. Both species possess a backward pointing crest-like spine near the summit of a highly inflated LA, and S3 is shallow over the sagittal axis. Palmer (1998b) distinguished the species based primarily on the form of L3: in *B. hermani*, the distal portion of L3 does not wrap around the anterolateral margin of L2 (and therefore S2 is roughly transverse), whereas in *B. brevispinus*, L3 wraps around L2 distally and S2 is kinked posteriorly near the axial furrow. Palmer (1998b, p. 665) also suggested that *B. brevispinus* has a “much more convex profile and steeper anterior margin of LA in lateral profile” and a “distinctly weaker development of S3” compared to *B. hermani*, although small sample size and different preservational modes render the reliability of these subtle features as species-diagnostic traits hard to assess. Nevertheless, the condition of L3 on the two known specimens of *B. hermani* has not been seen on any Cordilleran specimen, and *B. hermani* and *B. brevispinus* are herein provisionally regarded as distinct species (see also *B. cf. brevispinus*).

Bolbolonellus cf. brevispinus Palmer 1998b (Fig. 14C)

Material. FMNH PE58494.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10507, in the middle Monkton Formation.

Remarks. On this poorly preserved external mould of an incomplete cephalon, a crest-like spine projects posteriorly from the summit of a strongly inflated LA, and the distal portion of L3 wraps posteriorly around the anterolateral portion of L2 to give S2 a distinct caret shape on either side of the sagittal line. This combination of traits is characteristic of *Bolbolonellus brevispinus*, a species currently known only from upper Dyeran strata of Nevada and California (Palmer 1998b; Webster 2011a). The specimen is conservatively treated as *B. cf. brevispinus* on account of its poor preservational quality and incomplete nature.

Both Palmer (1998b) and Lieberman (1999) have commented on the possible synonymy of *Bolbolonellus brevispinus* and *B. hermani* (see discussion under the latter species). Unfortunately, the discovery of FMNH PE58494 does not unambiguously resolve this debate. The specimen demonstrates that a *B. brevispinus*-like form

occurs in the middle Monkton Formation, but it does not alter the diagnosis of either species unless it is interpreted as a *B. brevispinus*-like variant of *B. hermani*. This latter interpretation is not adopted herein because specimens of intermediate morphology between *B. brevispinus* and *B. hermani* are presently unknown.

Bolbolonellus sp. indet. (Fig. 14D, E)

Material. FMNH PE58493.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10507, in the middle Monkton Formation.

Remarks. This poorly preserved internal mould bears an LA morphology that is characteristic of *Bolbolonellus hermani* and *B. brevispinus*. However, the form of L3 cannot be determined on account of incomplete preservation, and species-level identification cannot be achieved.

Family UNCERTAIN

Olenelloid sp. indet. A (Fig. 14F)

Material. NYSM 18379.

Occurrence. Vermont: Colchester, Chittenden County: Unknown horizon within the Monkton Formation.

Remarks. This incomplete cephalon bears a short preglabellar field and a plectrum. The preserved portion is consistent with *Olenellus agellus*—a species otherwise not known from the Monkton Formation—but without knowledge of glabellar features even family-level assignment is impossible.

Olenelloid sp. indet. B (Fig. 14G, H)

Material. FMNH PE58497 and (tentatively) FMNH PE58492.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10508 and (tentatively) ICS-10507, in the middle Monkton Formation.

Remarks. FMNH PE58497 is very poorly preserved, but the proportionally short ocular lobes (with posterior tips located transversely opposite the lateral margins of the posterior third of L1) and the general outline of the glabella and cephalon are consistent with *Mesonacis vermontanus*. The general outline of the extraocular area on FMNH PE58492 is also consistent with *M. vermontanus*. However, without knowledge of glabellar features even family-level assignment is impossible for these specimens.

Olenelloid sp. indet. C (Fig. 14I)

Material. FMNH PE58500.

Occurrence. Vermont: Powerline section, Chittenden County: ICS-10508, in the middle Monkton Formation.

Remarks. This specimen is only a fragment of a cephalon, but is relatively well preserved compared to other material from the Monkton Formation such that a granular ornament is evident on the dorsal surface of the genal spine and the lateral cephalic border. The extraocular area is moderately strongly vaulted, and the ocular lobes are relatively long (the posterior tips are located at the posterior border furrow). A posterior ocular line is also present. These traits are suggestive of an affiliation to biceratopsids such as *Bristolia* spp. or to an olenellid such as *Olenellus fowleri*, but family-level assignment is impossible without

knowledge of glabella features.

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APPENDIX 1

Comments on stratigraphic nomenclature

Some of the stratigraphic nomenclature of this report differs from the Vermont Geological Map (Ratcliffe *et al.* 2011). A number of stratigraphic units in northwestern Vermont (e.g., Fig. 2) are lithologically heterogeneous lithosomes, and the designation “Formation” is herein applied to them following Dorsey *et al.* (1983). These include the Cheshire “Quartzite” (with black mudstone interbeds and commonly a feldspathic quartz arenite composition; e.g., Landing *et al.* 2007), the Dunham “Dolostone” (with red siltstone layers and upper dolomitic quartz arenites and arenaceous dolostones [“Mallett facies” of Shaw 1958; Fig. 2]), the Monkton “Quartzite” (with dolostone and dolomitic quartz arenite beds; e.g., the Powerline section of this report), the Winooski “Dolostone” (with beds of dolostone clast conglomerate, siliceous quartz arenites, and siliciclastic mudstone; e.g., Ratcliffe *et al.* 2011), and the Parker “Slate” (with massive dolostone intervals, dolostone debris flows, and dolostone nodules; e.g., Shaw 1958; this report).

The “Skeels Corners Slate” of the Vermont Geologic Map (Ratcliffe *et al.* 2011) follows Stone & Dennis (1964) and Dorsey *et al.* (1983, fig. 3), who greatly thickened Shaw’s (1958) “Skeels Corners Slate”, which was originally defined as bounded by the Mill River and Rockledge conglomerates (Fig. 2). Dorsey *et al.* (1983, fig. 3) and Ratcliffe *et al.* (2011) have created a homonym of “Skeels Corners” (see North American Commission on Stratigraphic Nomenclature 1983) by redefining it as a slaty unit that incorporates all of the Franklin Basin units above the Dunham Formation.

During field work for this report and in related studies (e.g., Landing 1983, 2007; EL unpublished data 2014), the stratigraphic divisions of Shaw (1958) and Stone & Dennis (1964) were generally found to be recognisable and mappable units in the Franklin Basin and in adjacent deposits of the Middlebury shelf. Thus, the absence on the Vermont Geologic Map of units such as the thick Saxe Brook Formation in the northern Franklin Basin (Ratcliffe

et al. 2011; see Fig. 2) is problematical in that it is an easily recognised, ridge-forming lithosome (Shaw 1958; Mehrtens & Dorsey 1987; Mehrtens & Hadley 1995). In addition, the Winooski Formation is herein regarded as extending north of the Lemoille River (*vide* Stone & Dennis 1964; Dorsey *et al.* 1983; Fig. 2), although it has been mapped as “massive dolostones” either at the base of the Rugg Brook Formation (Mehrtens & Hadley 1995) or comprising a unit of “massive dolostones” that are transitional to the south into similarly massive Winooski Formation dolostones (Ratcliffe *et al.* 2011, their unit “Cpdo”).

A number of published syntheses have not apparently been considered in the Vermont Geologic Map (Ratcliffe *et al.* 2011). Thus, the Monkton Formation is portrayed as a completely middle Cambrian unit in Ratcliffe *et al.* (2011), although its known faunas are upper lower Cambrian (Shaw 1962; Stone & Dennis 1964; Speyer 1983; this report). In addition, the unconformable contact of the Gorge and Highgate formations in the Franklin Basin (Landing 1983) must be regarded as the Cambrian–Ordovician boundary (Fig. 2). The definition of the base of the Ordovician at the base of the *Iapetognathus* Zone means that the Gorge

Formation does not extend into the Ordovician (*vide* Ratcliffe *et al.* 2011). Conodont-based biostratigraphic and lithologic study of the uppermost Cambrian and lowest Ordovician on the eastern New York–western Vermont shelf indicates that the Cambrian–Ordovician boundary is a regional sequence boundary, and that the Little Falls Formation (not the synonymous “Clarendon Springs Dolostone/Formation” and laterally equivalent non-dolomitised “Shelburne Marble”) is the uppermost Cambrian unit on the east Laurentian shelf (Landing *et al.* 2003, 2007; Landing 2007, 2012).

APPENDIX 2

The following table lists previous and current taxon assignments for olenelloid specimens from the Parker Formation. Specimens are arranged alphabetically by institution, then by specimen number. See main text for justification of identifications and explanation of institutional abbreviations. Locality abbreviations: G, Georgia, Vermont; GC, lower 10 feet of the Parker Slate, two miles west of Georgia Center, Vermont; KQ, Kelly quarry; PQ, Parker quarry; 25a, USNM Locality 25a, near Swanton, Vermont; 4789, Locality 4789.

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
AMNH 223	PQ	Whitfield, 1884, pl. 15, fig. 1 Walcott, 1910, p. 305 Bell, 1931, fig. 4 Resser & Howell, 1938, p. 223 Shaw, 1955, pl. 75, fig. 3 Lieberman, 1998, fig. 3.2 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Paedeumias transitans</i> <i>Olenellus thompsoni</i> <i>Olenellus agellus</i> <i>Olenellus brachycephalus</i> <i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i>
AMNH 225	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	not seen
AMNH 226 (515670)	PQ	Whittington, 1989, p. 114	<i>Olenellus thompsoni</i>	not seen
AMNH 227	PQ	Whitfield, 1884, pl. 15, fig. 2 Walcott, 1910, p. 305 Resser & Howell, 1938, p. 226 Shaw, 1955, pl. 75, fig. 1 Lieberman, 1998, fig. 3.3 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> (caption states <i>Olenellus vermontana</i>) <i>Paedeumias transitans</i> <i>Paedeumias perkinsi</i> <i>Olenellus brachycephalus</i> <i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i>
AMNH 228	PQ	Resser & Howell, 1938, p. 226	<i>Paedeumias perkinsi</i> ?	not seen
AMNH 230 (= USNM 62475; = FMNH UC15941)	PQ	Hall, 1859a, fig. 2 Hall, 1859b, figure on p. 527 Hall, 1860, figure on p. 117 Hall, 1862a, pl. 13 Resser & Howell, 1938, pl. 4, fig. 15	<i>Olenus vermontana</i> (holotype) <i>Olenus vermontana</i> (holotype) <i>Barrandia vermontana</i> (holotype) <i>Barrandia vermontana</i> (holotype) <i>Olenellus vermontanus</i> (holotype)	<i>Mesonacis vermontanus</i>
AMNH 231	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	not seen

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
AMNH 243	PQ	Lieberman, 1999, fig. 2.4	<i>Olenellus agellus</i>	<i>Olenellus agellus</i>
AMNH 243 (a second specimen?)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	not seen
AMNH 244 (= USNM 4795; = USNM 62474; = FMNH UC15942)	PQ	Hall, 1859a, fig. 1 Hall, 1859b, figure on p. 526 Hall, 1860, figure on p. 116 Hall, 1862a, pl. 13, fig. 1 Ford, 1881, fig. 12 Resser & Howell, 1938, p. 217, pl. 3, fig. 19 Resser & Howell, 1938, p. 223	<i>Olenus thompsoni</i> (holotype) <i>Olenus thompsoni</i> (holotype) <i>Barrandia thompsoni</i> (holotype) <i>Barrandia thompsoni</i> (holotype) <i>Olenellus thompsoni</i> (holotype) <i>Olenellus thompsoni</i> (holotype) <i>Olenellus agellus</i> (paratype) [probably a typo: see Lieberman, 1999, p. 17]	<i>Olenellus thompsoni</i>
AMNH specimen? (unspecified)	PQ	Whitfield, 1884, pl. 15, fig. 3 Walcott, 1910, p. 305 Resser & Howell, 1938, p. 226 Shaw, 1955, p. 791 Lieberman, 1998, p. 70	<i>Olenellus thompsoni</i> (caption states <i>Olenellus vermontana</i>) <i>Paedeumias transitans</i> <i>Paedeumias perkinsi</i> <i>Olenellus brachycephalus</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
AMNH specimen? (unspecified)	PQ	Whitfield, 1884, pl. 15, fig. 4 Walcott, 1910, p. 305 Resser & Howell, 1938, p. 223 Shaw, 1955, p. 791 Lieberman, 1998, p. 70	<i>Olenellus thompsoni</i> (caption states <i>Olenellus vermontana</i>) <i>Paedeumias transitans</i> <i>Olenellus agellus</i> <i>Olenellus brachycephalus</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
FMNH UC12981	G	New herein		<i>Olenellus agellus</i>
FMNH 14675 p41	G	New herein		<i>Olenellus transitans</i>
FMNH 14675 p42	G	New herein		<i>Olenellus agellus</i>
FMNH UC21291	PQ	New herein		<i>Mesonacis vermontanus</i>
FMNH UC23259	PQ	New herein		<i>Olenellus transitans?</i>
MCZ 1793	PQ	Lieberman, 1999, fig. 2.3	<i>Olenellus agellus</i>	<i>Olenellus agellus</i>
MCZ 2427	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
MCZ 2428	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 2429	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
MCZ 2431	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 2433	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 2433 (a second specimen?)	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	not seen
MCZ 2434	PQ	Lieberman, 1998, p. 67 Lieberman, 1999, p. 41	<i>Mesonacis vermontanus</i> <i>Mesonacis vermontanus</i>	<i>Olenelloid</i> sp. indet.

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
MCZ 2435	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
MCZ 2437	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2438	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2441 (two lots)	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	<i>Olenellus agellus</i> ?
MCZ 2444	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2443	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	<i>Olenellus agellus</i> ?
MCZ 2447	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2449	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2450	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2451	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	<i>Olenellus thompsoni</i>
MCZ 2451 (a second specimen?)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	not seen
MCZ 2453	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2455	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2459	PQ	New herein		<i>Olenellus transitans</i> ?
MCZ 2460	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	<i>Olenellus</i> sp. indet.
MCZ 2461	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2465	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
MCZ 2467	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	<i>Olenellus</i> cf. <i>agellus</i>
MCZ 2467 (a second specimen?)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	not seen
MCZ 2469 (two specimens)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	<i>Olenellus agellus</i>
MCZ 2470 (two specimens)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> (smaller specimen), <i>Olenellus</i> sp. indet.
MCZ 2471	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	<i>Olenellus agellus</i> ?
MCZ 2474	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> ?
MCZ 2476	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus</i> sp. indet.
MCZ 2478 (2 cephalae)	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i> (larger specimen tentatively assigned)

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
MCZ 2480	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 2482	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, pp. 15, 17	<i>Olenellus thompsoni?</i> <i>Olenellus agellus</i> or <i>Olenellus thompsoni</i>	<i>Olenellus agellus?</i>
MCZ 2522	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 3684	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	<i>Olenellus agellus?</i>
MCZ 7368	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
MCZ 7369	PQ	Lieberman, 1999, p. 17	<i>Olenellus agellus</i>	not seen
MCZ 52525 (formerly MCZ 2525)	4789	New herein		<i>Olenellus transitans</i>
MCZ 108661 (formerly MCZ 4994)	KQ	Shaw, 1955, pl. 75, fig. 2 Lieberman, 1998, p. 70 Lieberman, 1999, p. 15	<i>Olenellus brachycephalus</i> <i>Olenellus transitans</i> <i>Olenellus transitans</i>	<i>Olenellus transitans</i>
MCZ 108662 (formerly MCZ 4992)	KQ	Shaw, 1955, pl. 75, fig. 10 Lieberman, 1998, p. 67 Lieberman, 1999, p. 41	<i>Olenellus vermontanus</i> <i>Mesonacis vermontanus</i> <i>Mesonacis vermontanus</i>	Olenelloid sp. indet.
MCZ 113894 (formerly MCZ 5029)	GC	Lieberman, 1999, p. 139	<i>Bolbolenellus hermani</i>	Olenelloid sp. indet.
MCZ 193182, MCZ 193183 (formerly MCZ 2525)	4789	New herein		<i>Olenellus agellus?</i>
PUM 42012	VT	New herein		<i>Olenellus transitans</i>
USNM 14675.235z	PQ	New herein		<i>Olenellus agellus</i>
USNM 14675.236a (specimen 1)	PQ	Resser & Howell, 1938, pl. 9, fig. 11 Shaw, 1955, p. 793 Lieberman, 1998, p. 70 Lieberman, 1999, p. 15 Lieberman, 1999, p. 17	<i>Olenellus agellus</i> <i>Olenellus thompsoni</i> <i>Olenellus transitans</i> <i>Olenellus transitans</i> <i>Olenellus agellus</i>	<i>Olenellus transitans</i>
USNM 14675.236a (specimen 2)	PQ	New herein		<i>Olenellus</i> sp. indet.
USNM 15399a	PQ	Walcott, 1885, figs 1, 2 Walcott, 1886, pl. 24, fig. 1a, b Walcott, 1890b, pl. 87, fig. 1a, b Walcott, 1910, pl. 26, figs 1, 2, pl. 44, fig. 2 Resser & Howell, 1938, pl. 4, fig. 16 Palmer & Repina, 1993, fig. 3.2 Palmer & Repina in Whittington et al., 1997, fig. 255.2 Lieberman, 1999, p. 41	<i>Mesonacis vermontana</i> <i>Mesonacis vermontana</i> <i>Olenellus (Mesonacis)</i> <i>vermontana</i> <i>Mesonacis vermontana</i> <i>Olenellus vermontanus</i> <i>Olenellus (Mesonacis)</i> <i>vermontanus</i> <i>Olenellus (Mesonacis)</i> <i>vermontanus</i> <i>Mesonacis vermontanus</i> (neotype)	<i>Mesonacis vermontanus</i>
USNM 15399b	PQ	Walcott, 1910, pl. 26, fig. 3 Resser & Howell, 1938, p. 220	<i>Mesonacis vermontana</i> <i>Olenellus georgiensis</i>	<i>Mesonacis vermontanus</i>

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
USNM 15418a	PQ	Walcott, 1886, pl. 17, fig. 2 Lesley, 1889, text-fig. on p. 491, labeled pl. 17 Walcott, 1890b, pl. 83, fig. 1a Cole, 1892, fig. 1 Moberg, 1899, pl. 13, fig. 2 Walcott, 1910, pl. 34, fig. 9 Resser & Howell, 1938, pl. 3, fig. 17 Palmer & Repina, 1993, fig. 3.1 Palmer & Repina in Whittington et al., 1997, fig. 255.1	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus (Olenellus) thompsoni</i> <i>Olenellus (Olenellus) thompsoni</i>	<i>Olenellus thompsoni</i>
USNM 15418b	PQ	New herein		<i>Olenellus thompsoni</i>
USNM 15418c (= YPM 8189)	PQ	Lieberman, 1998, fig. 3.1	<i>Olenellus thompsoni</i>	<i>Olenellus thompsoni</i>
USNM 15419a	25a	Walcott, 1886, pl. 17, fig. 9 Lesley, 1889, pl. 17, fig. 9 on page 491 Walcott, 1890b, pl. 82, fig. 1a Walcott, 1910, pl. 35, fig. 4	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i>	<i>Olenellus</i> sp. indet.
USNM 56808a	PQ	Walcott, 1910, pl. 24, fig. 12, pl. 33, fig. 1, pl. 44, figs 7, 8 Resser & Howell, 1938, pl. 3, fig. 18 Shimer & Shrock, 1944, pl. 253, fig. 4 Poulsen in Harrington et al., 1959, fig. 132a, b Boardman et al., 1987, fig. 13.21i Whittington, 1989, figs 3–5, 7 Valentine, 2004, fig. 7.29a	<i>Paedeumias transitans</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus</i> <i>Olenellus thompsoni</i> <i>Olenellus</i>	<i>Olenellus thompsoni</i>
USNM 56808a (second specimen)	PQ	New herein		<i>Olenellus</i> aff. <i>transitans</i>
USNM 56808b	PQ	Walcott, 1910, pl. 34, fig. 1 Resser, 1928, p. 4 Resser & Howell, 1938, pl. 8, fig. 13 Shimer & Shrock, 1944, pl. 254, fig. 18 Poulsen in Harrington et al., 1959, fig. 135.5 Palmer & Repina, 1993, fig. 3.3 Palmer & Repina in Whittington et al., 1997, fig. 255.3	<i>Paedeumias transitans</i> <i>Paedeumias transitans</i> (lectotype) <i>Paedeumias transitans</i> <i>Paedeumias transitans</i> <i>Paedeumias transitans</i> <i>Olenellus (Paedeumias) transitans</i> <i>Olenellus (Paedeumias) transitans</i>	<i>Olenellus transitans</i>
USNM 90797	PQ	Resser & Howell, 1938, pl. 5, fig. 7 Lieberman, 1999, p. 41	<i>Olenellus georgiensis</i> (holotype) <i>Mesonacis vermontanus</i>	<i>Mesonacis vermontanus</i>
USNM 90797 (second specimen)	PQ	Resser & Howell, 1938, pl. 5, fig. 6 Shaw, 1955, p. 794 Lieberman, 1999, p. 41	<i>Olenellus georgiensis</i> <i>Olenellus vermontanus</i> <i>Olenellus thompsoni</i>	<i>Olenellus</i> aff. <i>fowleri</i>

Specimen Number	Locality	Figured or mentioned by...	As...	Identification Herein
USNM 90806.235x	PQ	Walcott, 1886, pl. 23, fig. 1 Walcott, 1890b, pl. 82, fig. 1 Walcott, 1910, pl. 35, fig. 1, pl. 44, fig. 9 Resser & Howell, 1938, pl. 9, fig. 12 Shaw, 1955, p. 793 Lieberman, 1999, p. 15 Lieberman, 1999, p. 17	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus agellus</i> (holotype) <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus agellus</i>	<i>Olenellus agellus</i>
USNM 90806.235y	PQ	Walcott, 1886, pl. 22, fig. 1 Lesley, 1889, text-fig. on p. 491, labeled pl. 22 Walcott, 1890b, pl. 83, fig. 1 Resser & Howell, 1938, pl. 9, fig. 13 Shaw, 1955, p. 793 Lieberman, 1999, p. 15 Lieberman, 1999, p. 17	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus agellus</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus agellus</i>	<i>Olenellus agellus</i>
USNM 90810 (formerly USNM 56836a)	PQ	Walcott, 1886, pl. 17, fig. 1 Walcott, 1890b, pl. 83, fig. 1b Walcott, 1910, pl. 35, fig. 8 Resser & Howell, 1938, pl. 7, fig. 2	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> <i>Olenellus crassimarginatus</i> (holotype) <i>Olenellus crassimarginatus</i> (holotype)	<i>Olenellus crassimarginatus</i>
USNM 90814 (first specimen)	PQ	Resser & Howell, 1938, pl. 8, fig. 1	<i>Paedeumias perkinsi</i> (holotype)	<i>Olenellus transitans</i>
USNM 90814 (second specimen)	PQ	New herein		<i>Olenellus transitans</i>
USNM 90814 (third specimen)	PQ	New herein		<i>Olenellus transitans</i>
YPM 8189	PQ	Lieberman, 1998, fig. 3.1 Lieberman, 1999, p. 15	<i>Olenellus thompsoni</i> <i>Olenellus thompsoni</i> (neotype)	<i>Olenellus thompsoni</i>
YPM 72900	PQ	Lieberman, 1998, p. 70 Lieberman, 1999, p. 17	<i>Olenellus transitans?</i> <i>Olenellus agellus</i> or <i>Olenellus transitans</i>	<i>Olenellus transitans?</i>
YPM 72905	PQ	Lieberman, 1999, fig. 2.5	<i>Olenellus agellus</i>	<i>Olenellus agellus</i>