Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization

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Morphological variation within the Early Cambrian olenelline trilobite *Olenellus gilberti* from the Pioche Formation of Nevada is partitioned into ontogenetic, static (non-ontogenetic), and taphonomic components, providing clearer understanding of the nature and sources of the variation. Such understanding is crucial for improved systematic, phylogenetic and evolutionary analyses of early trilobites. Compaction caused a significant change in mean form and an increase in shape variance, distorting many aspects of biological shape and shape variation. Morphologically mature specimens exhibited variation in many quantitative and qualitative aspects of cephalic morphology, in the distribution of prothoracic axial nodes, and in the number of opisthothoracic segments. The variance of two log-transformed size measures does not significantly increase over the first five sampled instars, a pattern interpretable either as the oldest known case of targeted growth in animal history, or as evidence of strong selection during early ontogeny. The magnitude of static cephalic shape variation does not significantly change during late ontogeny, also indicative either of developmental regulation of form or of selection against deviant phenotypes. The dominant structure of cephalic static shape variation is similar to the pattern of shape change during late portions of ontogeny: intraspecific heterochrony might therefore have been an important contributor to size-independent shape variation. For many traits, the developmental system was not well buffered against internal and/or external variation so that the resulting phenotype was not tightly canalized in the condition of those traits. However, other aspects of cephalic growth are consistent with having been under tight developmental regulation, which would not be indicative of general developmental ‘sloppiness’. This cautions against generalizing observations from a limited number of traits to the entire organism.

**Keywords**: Cambrian; canalization; evolution; ontology; Trilobita; variation

**Introduction**

Early Cambrian olenelline trilobites occupy a pivotal position at the base of the evolutionary history of the Trilobita Walch, 1771 (Whittington 1989; Fortey & Whittington 1989; Fortey 1990; Ramsköld & Edgecombe 1991; Fortey & Owens in Whittington *et al.* 1997; Fortey in Whittington *et al.* 1997; Fortey 2001; Lieberman 2002; Jell 2003; Paterson & Edgecombe 2006). Olenellines, and sometimes members of the genus *Olenellus* Hall, 1861 itself, have therefore been assumed to represent the basal (plesiomorphic) condition for the Trilobita in many traits, including the nature of hypostome attachment (Fortey 1990; Jell 2003), cephalic ecdysial sutures (Repina 1990; Geyer 1996; Fortey & Owens in Whittington *et al.* 1997; Fortey in Whittington *et al.* 1997; Jell 2003; Paterson & Edgecombe 2006), exoskeleton thickness (Fortey in Whittington *et al.* 1997), trunk tagmosis (Paterson & Edgecombe 2006), thoracic segment number (Fortey & Owens in Whittington *et al.* 1997), thoracic articulation type (Fortey in Whittington *et al.* 1997; Paterson & Edgecombe 2006), and the timing of exoskeletal mineralization during ontogeny (Fortey in Whittington *et al.* 1997). Documentation of the condition of such traits within olenellines, including the degree of variation in the traits amongst and within olenelline species, is therefore critical to our understanding of trilobite macroevolutionary history.

It is well established that intraspecific variation in morphological traits is highly relevant to evolutionary studies. Intraspecific variation (including phenotypic change during ontogeny) is a raw material upon which natural selection operates, and the magnitude and structure of such variation within a species can constrain the rate and
direction of phenotypic evolution (e.g. Simpson 1944; Kluge & Kerfoot 1973; Gould 1977; Alberch et al. 1979; Maynard Smith et al. 1985; Burger 1986; Wagner 1988; Schluter 1996; Wagner & Altenberg 1996; Beldade et al. 2002; Marroig & Cheverud 2005; Hallgrímsson & Hall 2005; Sniewkowski & Murphy 2006; Renaud et al. 2006; Hunt 2007; Hansen & Houle 2008; Eroukhmanoff & Svensson 2008; Webster & Zelditch 2011b), and affect the long-term survivorship of that species (Hopkins 2011; Kolbe et al. 2011). Hypotheses of phylogenetic relationships amongst taxa can be profoundly affected by consideration of ontogeny and intraspecific variation: ontogeny can be used to determine character state ordering, can shed light on arguments of homology and independence amongst characters of the adult, and can be a source of additional characters (e.g. Mabee 2000); and whether and how intraspecific variation is coded within cladistic analyses can have marked effects on the resulting cladogram topology (Nixon & Davis 1991; Stevens 1991; Wiens 1995, 1998, 2000, 2001; Rannala 1995; Wiens & Servedio 1997, 1998). Knowledge of phenotypic variation is also critical for systematic palaeontology: only by studying the range of intraspecific variation within single spatiotemporally constrained samples can morphological differences between samples be defensively interpreted as representing either intraspecific variation or interspecific disparity. Study of the degree and pattern of variation (including ontogenetic change) within trilobites is therefore crucial to our understanding of particular evolutionary trends or events and to phylogenetic reconstruction, as well as to issues such as species diagnosis, diversity estimation, and biostatigraphical correlation (e.g. McNamara 1978, 1986; Hughes 1991, 1994; Webster et al. 2001; Webster & Zelditch 2005, 2011a, b; Adrain & Westrop 2006; Webster 2007a, b, 2009a, 2011a; Hopkins & Webster 2009). The need for detailed characterization of the nature and magnitude of intraspecific variation is magnified for olenellines given their basal phylogenetic placement within the Trilobita (above) and the well-known difficulty in establishing robust diagnoses of, and hypotheses of relationship amongst, olenelline species and higher taxa (Palmer & Halley 1979; Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Lieberman 1998, 1999).

Despite this need, there have been very few quantitative studies of olenelline intraspecific variation and ontogeny, and interpretations of the data are mixed. Some workers have claimed that olenellines exhibited a high degree of intraspecific variation relative to more derived trilobites, based on non-quantitative observations of variation in the shape and size of various cephalic features (Palmer & Halley 1979), meristic variation in thoracic segment number (McNamara 1986), and the frequency of intraspecific polymorphisms coded in cladistic analyses (Webster 2007a). These observations have been levied as support for a hypothesis that developmental processes were less buffered against internal and/or external sources of variation, and the resulting phenotypes thus less tightly canalized, in early trilobites (McNamara 1986; see also Hughes 1991, 1994) although alternative or complementary ecological explanations are equally plausible; (see Webster 2007a). However, quantitative morphometric data have been used to discriminate some olenelline species (e.g. Best 1952; Riccio 1952; Palmer 1957; Poulsen 1974; Cowie & McNamara 1978; McNamara 1978; Lieberman 1998; Webster 2007b, c, 2009a), suggesting that intraspecific variation was not so large as to completely blur taxonomic distinctions or obfuscate phylogenetic signals (see also comments by Palmer 1998, p. 656 and Lieberman 1998, p. 63). There is therefore a premium on studies that document the structure and magnitude of variation within olenelline species, particularly studies that are able to (1) parse the variation into ontogenetic, static (non-ontogenetic), and taphonomic components and thus lead to a better understanding of olenelline palaeobiology; and (2) determine whether olenelline phenotypes were weakly canalized relative to other trilobite clades and thus provide critical empirical data for incorporation into macroevolutionary theory.

The present paper documents the morphology and the structure and degree of morphological variation in *Olenellus gilberti* Meek in White, 1874 over much of its ontogeny, from sagittal cephalic length of 0.6 mm to more than 64 mm. Non-compacted, silicified specimens are used to study variation in qualitative and quantitative traits through ontogenetic development. Compacted but otherwise exquisitely preserved material recovered from shale provides data pertaining to variation in qualitative and quantitative traits amongst morphologically mature specimens. Comparison of the two samples provides insight into the effects of taphonomic compaction on fossil morphology. Variation in cephalic shape and size is quantified for each of several ontogenetic stages, permitting a test of whether patterns of variation through ontogeny are consistent with the hypothesis of weakly canalized development. The ontogeny of *O. gilberti* is compared to that of other olenellines, and the degree of variation within *O. gilberti* is compared to that of other trilobites, so as to determine whether *O. gilberti* is in any way unusual in these aspects of palaeobiology. This is the most detailed study of olenelline morphology, development, and intraspecific variation undertaken to date. Data presented herein provide an empirical benchmark of ontogenetic, static, and taphonomically induced intraspecific variation that not only will guide future studies of olenelloid systematics and phylogeny, but also represents a useful advance towards a fuller understanding of early trilobite palaeobiology and evolution.

**Previous work**

*Olenellus gilberti* was, until recently, a poorly diagnosed species with purported occurrences in upper Dyeran
(traditional upper ‘Lower Cambrian’ of Laurentia) strata of Nevada, Utah, California, Idaho, northern Mexico, Alberta, British Columbia and (tentatively) north-west Greenland (see below). However, Palmer (1998) revised the species based on newly discovered, abundant material of exquisite preservational quality from Nevada (see below), and restricted its occurrence to localities in the southern Great Basin. Additional fieldwork conducted since 1998 has increased the number of localities within the southern Great Basin from which O. gilberti is known and has refined its stratigraphical occurrence to the upper Bolbolenellus euryaparia Zone and succeeding Nephrolellus multinodus Zone, within upper Dyeran depositional sequences III and IV (Webster 2011b); a comprehensive list of currently accepted occurrences, including many discoveries made since 1998, is provided in the Systematic palaeontology section herein. Early claims of extreme coveries made since 1998, is provided in the Systematic list of currently accepted occurrences, including many dis-sequences III and IV (Webster2011b); a comprehensive Zone, within upper Dyeran depositional nellus multinodus

Bolbolenellus euryparia

and has refined its stratigraphical occurrence to the upper

Olenellus gilberti

Webster, 2007c (see Walcott 1910; Palmer & Halley Bristolia Harrington, 1956, and Paranephrolenellus Webster, 2007c (see Walcott 1910; Palmer & Halley 1979; Webster 2007c).

The exquisite material described by Palmer (1998) was collected from two localities: the Ruin Wash Lagerstätte (yielding compacted but otherwise well-preserved and often articulated specimens of large size preserved in shale), and a nodular carbonate bed from nearby Hidden Valley (yielding non-compacted but almost invariably disarticulated silicified specimens of a wide range of sizes) (Figs 1, 2). Palmer’s (1998) description of the mature morphology of O. gilberti was relatively detailed and did consider the range of intraspecific variation. In fact, the work established O. gilberti as one of the best-studied olenellines to date. The present work builds upon and expands beyond Palmer’s (1998) earlier work by (1) exploiting additional specimens collected from those same localities and thus increasing sample size; (2) applying an arsenal of quantitative morphometric techniques to supplement the more traditional qualitative description of form and variation in form; and (3) providing the first detailed description of the ontogeny of the species. Regarding this last point, material on which previous descriptions of the ontogeny of ‘O. gilberti’ were based have since been reassigned to other species. Walcott (1910, p. 328, pl. 36, figs 11–15) illustrated and described a series of morphologically immature cephala from Parmigan Pass, Alberta, that clearly differs from the material described herein (most obviously by possessing procranial spines) and that was correctly excluded from O. gilberti by Palmer & Halley (1979; also Palmer 1998). The silicified material described as ‘O. gilberti’ in the classic work of Palmer (1957) has since been reassigned to O. fowleri Palmer, 1998 (see Palmer 1998) and more recently to O. aff. fowleri (see Webster 2011b, c). Similarly, the ontogenetic sequence from Cranbrook, British Columbia, assigned to ‘O. gilberti’ by Hu (1985) has since been reassigned to a new and as-yet-undescribed species of Olenellus (see Palmer 1998). Under the current concept of the species, Palmer (1998, p. 668, figs 8.4, 8.6–8.8) presented only a very limited summary of the ontogeny of O. gilberti, illustrating just four silicified cephalia and mentioning only the low relief of the glabella and ocular lobes, the absence of procranial spines, and the presence of intergenal spines that are cylindrical rather than ventrally open in transverse cross section. Palmer (1998, p. 656) deferred detailed work on the silicified material pending a more comprehensive evaluation of olenellid ontogenies. The present author is conducting just such an evaluation as part of an ongoing research program on early trilobite evolution (Webster 1999, 2003, 2007b, e, 2009a; Webster et al. 2001; Webster & Zelditch 2005), and a detailed study of the ontogeny of O. gilberti can now be fruitfully discussed within a broader comparative framework.

A comparative framework of olenellloid ontogeny

Trilobite ontogeny is traditionally subdivided into the protaspis, meraspid and holaspis periods based on the nature of trunk articulation (reviewed by Chatterton & Speyer in Whittington et al. 1997; Hughes et al. 2006; Hughes 2007). As is typical for silicified olenelloids (Palmer 1957; Palmer & Halley 1979; Webster 2007b) the material studied herein is almost invariably disarticulated, and knowledge of the early ontogenetic development of Olenellus gilberti is restricted to cephalic morphology alone. Beyond the fact that all specimens are post-protaspis (because even the smallest sampled specimens possess a posterior cephalic margin against which the trunk would have articulated), the traditional subdivisions of trilobite ontogeny cannot be applied to the material studied herein: isolated cephalia cannot be assigned to particular meraspid degrees, and the meraspid/holaspis transition cannot be identified. Ontogenetic development of the olenellloid cephalon has been divided into five distinct and successive phases (summarized below; Webster et al. 2001; Webster 2007b, c, 2009a). The relationships between these phases of cephalic development and several other previously proposed subdivisions of trilobite ontogeny were discussed by Webster (2007b, pp. 1170–1171) and are not repeated here.

Cephalia in phases 1 and 2 of development are charac-
terized by an absence of genal spines, by a glabella that slightly tapers anteriorly between glabellar furrows S1 and S3, and by ocular lobes that do not contact glabellar lobe L3. The distinction between phases 1 and 2 was first recognized in studies of Nephrolenellus multinodus Palmer in Palmer & Halley, 1979 and N. geniculatus...
Figure 1. Geographical provenance of the material studied herein. A, map of the southern Great Basin, showing the location of upper Dyeran localities from which *Olenellus gilberti* has been recovered. Localities are shaded according to their general position on the Cambrian shelf, as discussed by Webster (2011b). Black line with triangles marks the eastern limit of the Sevier Thrust Belt (overthrust blocks to the west). Abbreviations: DR, Desert Range; EC, Echo Canyon section, Funeral Mountains; EM, Eagle Mountain; FM, Frenchman Mountain; GR, Groom Range; GS, Grassy Spring section, Delamar Mountains; HR, Highland Range (including One Wheel Canyon section); HV, Hidden Valley section, Burnt Springs Range; KG, Klondike Gap, Chief Range; MM, Marble Mountains; OSS, Oak Spring Summit section, Delamar Mountains; PH, Pioche Hills (type locality); PP, Pyramid Peak section; RS, Resting Springs Range; RW, Ruin Wash section, Chief Range; SM, Split Mountain, Clayton Ridge; SOS, Seven Oaks Spring, Burnt Springs Range; TC, Titanotherium Canyon, Grapevine Mountains. B, detailed map showing location of Ruin Wash locality (Chief Range, Lincoln County, Nevada). The site has been excavated at several trenches (RW-1 to RW-3, ‘taphonomy trench’) as discussed by Webster *et al*. (2008). C, Detailed map showing location of Hidden Valley locality (Burnt Springs Range, Lincoln County, Nevada). Site of nearby Seven Oaks Spring locality is also shown. Maps in 2 and 3 created with TOPO! software © National Geographic 2002; www.nationalgeographic.com/topo).
Palmer, 1998 (Webster et al. 2001; Webster 2007b). It is based on a change in the rate of transverse elongation of the posterior cephalic margin relative to increase in cephalic length, the rate first decreased (phase 1) then increased (phase 2). When the phase 1 to phase 2 transition cannot be unambiguously identified, either because the change in rate of cephalic widening relative to cephalic lengthening is not apparent (as for *O. gilberti*, herein) or because small sample size currently precludes detailed analysis of growth dynamics (as in the vast majority of olenelloid species), then immature cephalia lacking genal spines can only be assigned to ‘pre-phase 3’ of development. The other notable morphological change during phases 1 and 2 of cephalic development involved the initial development of an extraocular area between the ocular lobes and the lateral cephalic border. Glabellar...
shape change during phases 1 and 2 of cephalic development was minimal.

Entry into phase 3 of cephalic development was defined by the first appearance of genal spines. Morphological change during phase 3 included a widening (tr.) of the extraocular area and an elongation (tr.) of the posterior cephalic margin. The genal spines progressively elongated and the intergenal spines progressively shortened. The glabella underwent pronounced shape change during phase 3: LO widened and lengthened so that the glabella tapers evenly anteriorly to L2 or S3 on late phase 3 cephala; LA proportionally expanded (tr. and sag.); and L3 proportionally shortened (exsag.) and widened (tr.) anteriorly so that the anterolateral corners of L3 contact the adaxial margin of the ocular lobes.

Entry into phase 4 of cephalic development was defined by the onset of pronounced lateral widening (tr.) of L3 relative to L2 and LA, so that the glabella became transversely narrowest at L2. Lateral expansion of L3 led to an increasing extent of contact between the anterolateral margins of L3 and the inner margin of the ocular lobe and/or LA. In some taxa (e.g. species of *Nephrolenellus* Palmer & Repina, 1993) this ultimately resulted in the merger of these structures and the isolation of S3 from the axial furrow (but not in other taxa, such as species of *Paranephrolenellus*). Other morphological changes during phase 4 included continued elongation (tr.) of the posterior cephalic margin, including in the region between the intergenal and genal spines; continued proportional expansion of LA in all directions; continued proportional widening (tr.) of L3; a proportional shortening (exsag.) of L2; and a slight proportional lengthening (exsag.) of L1. Some genera terminated cephalic development in phase 4 (e.g. *Nephrolenellus*; Webster 2007b).

Entry into phase 5 of cephalic development was defined by the onset of pronounced proportional lateral widening (tr.) of L2, so that the glabella became transversely narrowest at S1. In some taxa (e.g. *Peachella* Walcott, 1910, *Eopeachella* Webster, 2009a, *Olenellus*, most species of *Bristolia*) the lateral expansion of L2 resulted in the distal merger of the anterolateral portion of L2 with the posterolateral portion of L3, and the corresponding isolation of S2 from the axial furrow.

The sequential order of the phase-defining events is conserved – and the five phases of cephalic development are deemed to be homologous – across all olenelloid species studied to date. The five-phase scheme of subdividing cephalic development therefore offers a useful framework for describing and comparing olenelloid cephalic ontogeny. The ontogeny of *O. gilberti* is herein described and quantitatively analysed using this framework. The present study is the first to perform detailed geometric morphometric analyses of patterns of shape change during phase 5 of cephalic development of an olenelloid trilobite. (Low sample size of large cephala of previously studied species necessitated that patterns of shape change during phase 5 in those species were documented only in descriptive terms or were analysed using only bivariate plots of traditional morphometric data [Palmer 1957; Webster 2007c, 2009a].) The analyses reveal that *O. gilberti* underwent a subtle but significant change in the pattern of ontogenetic shape change of the glabella during phase 5 that has not been identified in other olenelloid species studied to date. Detailed study of additional species (in progress) will determine whether this change is unique to *O. gilberti* or is more general amongst olenelloids. Pending determination of its generality, it is premature to use this change in ontogenetic allometry to define entry into a distinct ‘phase 6’ of cephalic development in olenelloid trilobites. Instead, this change in allometric patterning is herein used to differentiate an ‘early phase 5’ from a ‘late phase 5’ of cephalic development in *O. gilberti*. Specimens in late phase 5 of development (sagittal cephalic length > 9.3 mm) are treated as morphologically mature.

**Material and methods**

**Material**

Detailed qualitative observations and/or quantitative morphometric data were gathered for more than 680 silicified specimens and more than 500 non-silicified specimens of *Olenellus gilberti*. The stratigraphical and geographical separation of the sources for the silicified and non-silicified samples is small (Figs 1, 2), and the primary source of morphological difference between conspecific fossils is more general amongst olenelloids. Pending determination of its generality, it is premature to use this change in allometric patterning to define entry into a distinct ‘phase 6’ of cephalic development in olenelloid trilobites. Taphonomic compaction has a significant impact on fossil form (Webster & Hughes 1999; also herein) that can overprint and distort subtle aspects of ontogenetic shape change. All quantitative analyses of ontogenetic shape change up to and including early phase 5 of cephalic development are therefore based entirely on the non-compacted, silicified material unless specified. However, silicified material is almost invariably disarticulated, and the maximum size of intact silicified cephalohid is much smaller than the maximum size of non-silicified cephalohid preserved in shale (Fig. 3). Study of the non-silicified sample therefore allows a more complete description of the ontogeny of *O. gilberti* by providing information regarding the morphology of the trunk and of large cephalohids. Quantitative analyses of ontogenetic shape change during late phase 5 of cephalic development necessarily are based on the compacted, non-silicified material.

All silicified specimens studied herein were collected from a single bed of nodular (ribbon) carbonate exposed at Hidden Valley, Burnt Springs Range, Lincoln County, Nevada (collections ICS-1173 and UCR 9963; Fig. 1). This bed is correlative with the ribbon carbonate immediately underlying the Ruin Wash Lagerstätte (Fig. 2;
fossils are extremely fragile, and it is unlikely that silicification itself imparted robustness against compaction. This suggests that the carbonate nodules grew and lithified at a relatively early diagenetic stage (before extensive dewatering and compaction), and thus protected the entombed fossils from being crushed. This hypothesis of early formation of the nodules is also supported by studies of primary bedding surfaces within them (Velechovsky 1985; Webster et al. 2008). Broken edges of damaged trilobite specimens reveal that the replaced exoskeleton is sometimes composed of two thin films of silica separated by a very thin void. The silica therefore crystallized inwards from the walls of the void left after dissolution of the exoskeleton and (at least sometimes) failed to meet in the middle. This adds to the delicacy of the fossils. Silt and sand grains that were entrapped within the growing carbonate nodule are often cemented to the surface of the silicified fossils and cannot be removed even by vigorous brushing under water. These impart a coarse, grainy texture to the fossils. Smaller specimens appear relatively more coarsely preserved than larger specimens because the former are closer in absolute size to the welded grains. Details of the exoskeleton, including ornament, are still discernable on most specimens despite the grainy preservation. Specimens exhibiting a problematic degree of grainy preservation (that obscured biological details of the exoskeleton) were excluded from morphometric analyses.

All non-silicified specimens studied herein were collected from the Ruin Wash Lagerstätte in the Chief Range, Lincoln County, Nevada (collections ICS-1044 and UCR 9945; Fig. 1). The trilobites in these collections are preserved as high quality, non-testate internal and external moulds in a 0.43 metre-thick interval of shale. The shale interval immediately overlies a nodular (ribbon) carbonate that is correlative with the bed at Hidden Valley from which the silicified fossils of *O. gilberti* studied herein were recovered (above; Fig. 2). The nodular carbonate and overlying shale together comprise a stratigraphically thin (0.67 metres at Ruin Wash) deepening-to-shallowing sequence (upper Dyeran depositional sequence IV of Webster 2011b, c; see also Webster et al. 2008). The entire deepening-to-shallowing sequence was deposited within an already deep subtidal setting, perhaps entirely below storm wave base (Webster et al. 2008; Webster 2011b). Palmer (1998) presented the initial documentation of trilobites from the Ruin Wash Lagerstätte, and a more detailed account of the trilobite taphonomy and microstratigraphy of the site was provided by Webster et al. (2008). The trilobites in both the shale and the underlying carbonate appear not to have been transported, although current-driven bioclast alignment and sediment winnowing is evident in some intervals. Specimens within the shale are often fractured, and thus experienced compaction-related deformation prior to dissolution of the

**Figure 3.** Histograms depicting size-frequency distribution of *Olenellus gilberti* specimens studied herein. Size is here quantified as sagittal cephalic length (estimated for some incompletely preserved specimens). **A**, silicified specimens from Hidden Valley (*n* = 569); **B**, non-silicified specimens from Ruin Wash (*n* = 506). Data were also gathered from some larger specimens (silicified specimens ranging up to approximately 6.7 mm in sagittal glabellar length; non-silicified specimens ranging up to > 64 mm in sagittal glabellar length; see Fig. 6), but those specimens were fragmentary and their sagittal cephalic length could not be estimated with reasonable replicability so they are not included in these histograms. Note the different scale of the histograms.

Webster et al. 2008, fig. 4). (The nodular carbonate underlying the Ruin Wash Lagerstätte also contains silicified trilobites, but these do not reach the same maximum size as those from collection ICS-1173 and thus offer a less comprehensive sampling of ontogeny.) The silicified specimens occur within the nodules, which are composed of micritic carbonate with minor quartz silt and sand. The silicified fossils exhibit strong three-dimensional relief with no evidence of fracturing, and must have been sheltered from the effects of taphonomic compaction. The
exoskeleton. Some voids apparently served as depositional centres for the growth of wafer-thin ‘calcite haloes’ so that the sclerites appear to be replaced by and entombed within calcite (discussed by Webster et al. 2008, p. 107). No specimens within any of the samples exhibit symptoms of tectonic deformation. Poorly preserved specimens were not included in morphometric analyses. The effects of compaction on the morphology of O. gilberti were studied by Webster & Hughes (1999) and are further explored herein.

Collections ICS-1044 and UCR 9945 include trilobites collected from the entire 0.43-metre shale interval, and represent a within-habitat, time-averaged assemblage (Kidwell & Bosence 1991; Webster et al. 2008). The entire 0.43-metre shale interval likely accumulated over a timescale of decades to a few thousand years (Webster & Hughes 1999; Webster et al. 2008). The amount of time represented by the underlying nodular carbonate bed (including collections ICS-1173 and UCR 9963) is likely to be of a similar scale. Thus, although neither the silicified nor the non-silicified samples analysed herein represent a true ecological census of co-occurring individuals, the amount of microevolutionary change within and between the samples is assumed to be negligible. The fact that discrete instar clusters can be recognized within the silicified sample (see below) substantiates this assumption: a high rate of morphological evolution relative to the time represented by a single sample is expected to increase apparent phenotypic variance and potentially blur instar distinctions within that sample (Hunt & Chapman 2001; Hunt 2004).

**Institutional abbreviations**

All specimens examined herein are housed in the collections of: **ICS**: Institute for Cambrian Studies, Department of the Geophysical Sciences, University of Chicago; **FMNH**: Field Museum, Chicago; **UCR**: the geology museum at the University of California, Riverside; **CMC**: Cincinnati Museum Centre; and **DMNH**: Denver Museum of Natural History. More than 400 additional specimens of *O. gilberti* from the Ruin Wash Lagerstätte held in the collections of **MCZ**: Museum of Comparative Zoology, Harvard University; and **YPM**: Peabody Museum, Yale University were cursorily examined but detailed qualitative observations and quantitative morphometric data were not recorded.

**Terminology**

Morphological terminology largely follows that of Whittington & Kelly in Whittington et al. (1997), with modifications to olenelline thoracic and cephalic terminology proposed by Palmer (1998) and Webster (2007b), respectively. Following Webster (2007c, 2009a), genal spine advancement is measured by finding the point at which the axial furrow of the glabella is intersected by a transverse line drawn between the adaxial margins of the genal spine bases where they contact the posterolateral cephalic margin. The qualitative location of this point of intersection relative to the contact of glabellar lobes and furrows with the axial furrow is expressed in the descriptions. Following Webster (2009a), the ‘slot position’ of glabellar furrow S2 or S3 refers to a location along that furrow approximately midway (tr.) between the sagittal axis and the axial furrow. The five sequential ontogenetic phases of cephalic development of olenelloid trilobites are defined above. ‘Olenelline’ ‘olenelloid’, and ‘olenellid’ refer to the progressively less inclusive clades “Olenellina” Walcott, 1890 (probably paraphyletic), Olenelloidea Walcott, 1890, and Olenellidae Walcott, 1890, respectively (classification following Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Adrain 2011).

**Traditional morphometric analyses of cephalic shape variation**

Morphometric analysis of length and angle measurements has a long tradition in trilobite systematics (e.g. Lochman 1947; Best 1952; Riccio 1952; Shaw 1956, 1957; Palmer 1957; Temple 1975) and continues to be useful today (e.g. Webster 2007c, 2009a, b). Unlike landmarks in geometric morphometric analyses (below), traditional morphometric variables can be studied individually or in pairs as well as in a multivariate analysis. Incompletely preserved specimens from which data for only a subset of all variables can be digitized can therefore be included in at least some analyses of traditional morphometric data. Sample size in traditional morphometric analyses therefore tends to be higher than in multivariate analyses.

Traditional morphometric data were taken from digital images of 608 silicified and 220 non-silicified specimens of *Olenellus gilberti* from Hidden Valley and Ruin Wash, respectively. 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 cephalha). Values for variables relating to transverse measurements that span the sagittal axis were obtained on some specimens by doubling a transverse measurement from the sagittal axis to one end-point of the variable. Measurement errors introduced through these approximations are comparable in scale to left–right asymmetries on well-preserved specimens, and are deemed to be negligible. Univariate and bivariate visualization and analyses of traditional morphometric data were performed in the R software package (R Development Core Team 2012; http://www.r-project.org/).
Geometric morphometric analyses of cephalic shape variation

Landmark-based geometric morphometrics offers a powerful suite of tools for quantifying biological shape, shape variation, and covariation of shape with other biotic or abiotic variables or factors (e.g. Rohlf & Slice 1990; Bookstein 1991; Dryden & Mardia 1998; Webster & Sheets 2010; Zelditch et al. 2012). Geometric morphometric analyses are being used with increasing frequency to quantify patterns of ontogenetic shape change in trilobites (e.g. Webster 2007b and references therein, 2011a; Hopkins & Webster 2009; Bignon & Crónier 2012) and have recently been employed to study subtle aspects of development such as cephalic integration (Webster & Zelditch 2008, 2009, 2011a, b). Geometric morphometric techniques are employed herein to quantify cephalic shape variation within Olenellus gilberti, including that resulting from ontogenetic shape change and taphonomic compaction.

Cephalic shape is here summarized by digitizing the x- and y-coordinates of a series of discrete anatomical loci (landmarks) on the cephalon, recognizable and homologous on all specimens included within a given analysis. Coordinates of homologous landmarks on the left and right side of the cephalon were digitized, but those on the left side were subsequently computationally reflected across the sagittal axis and averaged with those of the homologous landmark on the right side. This reflecting-and-averaging procedure is desirable because it reduces data redundancy (left-right asymmetry is not a focus of the present study) and it allows inclusion of specimens that lack one member of a homologous landmark pair (the coordinates of the single landmark are used in place of the averaged coordinates of the pair). Landmark data were extracted from digital images of 171 sufficiently well-preserved silicified cephalon from Hidden Valley and 220 sufficiently well-preserved non-silicified cephalon from Ruin Wash using ImageJ (above). Some landmarks are inapplicable to certain developmental stages (e.g. the landmark at the intersection of S2 and the axial furrow is not defined on cephalon in phase 5 of development because at that stage S2 is isolated from the axial furrow). Different subsets of landmarks were therefore used to analyse shape change over different portions of ontogeny (see Webster et al. (2001) and Webster (2007b) for similar situations). Superimposition of landmark configurations of different specimens (translated, rotated, and rescaled according to the generalized least-squares (GLS) partial Procrustes optimization [see review by Webster & Sheets 2010 and references therein]) permits visual and statistical analysis of difference in cephalic shape. Analyses of the landmark data were conducted using software in the Integrated Morphometrics Programs (IMP) package, compiled by H. D. Sheets and freely available electronically at http://www3.canisius.edu/~sheets/moremorph.html (see Zelditch et al. 2012) and Webster & Sheets (2010) for practical guides to the IMP software.

Shape variation amongst landmark configurations digitized from 10 different images of the same specimen was two orders of magnitude smaller than shape variation amongst a sample of conspecific specimens of a similar size (true for silicified and for non-silicified specimens; data not presented). Measurement error associated with the mounting of specimens for photography and digitizing replicability is therefore deemed negligible.

Morphospace distortion introduced by projecting data from nonlinear shape space into a linear tangent plane for statistical analysis is negligible. For a configuration consisting of seven glabellar landmarks (silicified specimens, \(n = 116\)) the correlation between partial Procrustes distance and distance in the tangent-plane is extremely strong (1.000) with a slope of 0.999 (calculated using the program tpsSmall [Rohlf 2003], available at http://life.bio.sunysb.edu/morph/). Identical results were obtained for a configuration consisting of 12 cephalic landmarks (silicified specimens, \(n = 54\)). (See Webster & Sheets (2010) and references therein for a discussion of this issue of distortion.)

The centroid size of a landmark configuration is used as a measure of cephalic size. Centroid size is the square root of the sum of squared distances between each landmark and the centroid of a configuration (Bookstein 1991; see review by Webster & Sheets 2010). The precise (and surely nonlinear) relationship between size and true (chronological) developmental age is not known for any trilobite, but is assumed to be positive. Specimens that differ in centroid size for a given landmark configuration are therefore assumed to differ in developmental age.

The amount of difference in shape between two landmark configurations is quantified as the partial Procrustes distance (\(D_p\); the square root of the summed squared distances between corresponding landmarks on the configurations following GLS partial Procrustes superimposition; Bookstein 1991; see review by Webster & Sheets 2010). Model II regression of \(D_p\) (of all configurations relative to a designated reference configuration representing a morphologically immature cephalon) against centroid size therefore reveals the ‘rate’ (as a function of size rather than of time) of shape change away from that immature form. Statistical comparisons of these reduced major axis regression coefficients were performed using the smatr package (version 3.2.6; Warton et al. 2012) in R.

Shape variation is explored through a principal components analysis (PCA) of shape data using PCAGen6p (Sheets 2007a). The shape data utilized herein are partial warp scores (including the two uniform terms) calculated for each configuration in a sample using the consensus of all configurations in that sample as the reference form (see Webster & Sheets 2010) and references within for...
details). For any landmark configuration, each warp score quantifies the contribution of a mathematically independent style of deformation (a warp or one of the two uniform components) of the reference form to the shape difference between the reference and that configuration. Following PCA of the shape data, each resulting principal component (PC) is a mathematically independent axis of shape variation and can be described in terms of its effect on particular regions of the configuration. However, the PCs do not necessarily relate to biologically independent modes of variation. Actual shape variation within a given anatomical region is described by the net effect of all PCs upon that region.

Ontogenetic shape change is quantified as a multidimensional vector describing shape differences between superimposed landmark configurations of conspecific individuals of different size. Each element of the vector represents a pattern of landmark offset between superimposed landmark configurations (the regression coefficients of shape (shape coordinates or warp scores) on centroid size, normalized to unit length). Modification to patterns of shape change during ontogeny (ontogenetic allometric repatterning) is assessed by calculating an angle between vectors of shape change for successive phases of ontogeny (the arccosine of the dot product of the normalized ontogenetic vectors: see Webster et al. 2001; Webster 2007b; Zelditch et al. 2012). A statistically significant angle between successive phases of ontogeny (compared to the range of angles expressed within each phase, assessed by bootstrap resampling; Webster et al. 2001; Zelditch et al. 2003, 2012; Webster 2007b, 2011a) indicates that the pattern of growth differed between the phases. Vectors of shape change were calculated from Bookstein coordinates (following superimposition using Bookstein registration) and from warp scores generated through thin-plate spline analysis (TPS) of configurations (see Webster & Sheets 2010 and references therein for a review of these shape variables; and Webster et al. 2001, Webster & Zelditch 2005, Webster 2007b, 2011a, and Bignon & Crönier 2012) for previous applications of this technique to trilobites. Conclusions of analyses were robust to changes in designated baseline landmarks (for vectors derived from Bookstein coordinates) and reference form (for vectors derived from warp scores), and results based on vectors calculated from Bookstein coordinates were almost invariably congruent with results based on vectors calculated from warp scores (data not presented). Only results from analyses involving calculation of vectors from warp scores are therefore presented herein. Multivariate regression of shape on size to obtain ontogenetic vectors was performed using Regress6N (Sheets 2008). Calculation of the angle between ontogenetic vectors of shape change was performed using VecCompare6c (Sheets 2003a).

Mean shape and shape variation for a particular phase of ontogeny was calculated using size-standardization. Size-standardization is an analytical procedure that removes shape variation resulting from size variation, thus permitting an estimation of "static" shape and shape variation within a sample (i.e. with allometric variation amongst individuals removed). The procedure involves performing a linear regression of shape variables (warp scores) against size (the natural log of centroid size, lnCS), then using this model to predict the shape of each specimen at a user-specified size. Residuals (shape deviations from the regression) remain associated with each specimen, so that the size-standardized shape of each specimen is the predicted shape of that specimen at the user-specified size plus its original residuals. When all specimens within a sample are size-standardized to the same log centroid size, shape variation is determined entirely by the residuals from the regression model and shape variation attributable to the regression (i.e. to allometry) has been removed. This technique has been previously employed in trilobite studies (e.g. Hopkins & Webster 2009; Webster 2011a, Webster & Zelditch 2011a, b). Size-standardization was performed using the Standard6 software (Sheets 2001).

Difference in mean shape between two samples can be quantified as the partial Procrustes distance (above) between the consensus configurations of those samples. The significance of the observed difference between samples means must be determined in light of the shape variation within those samples. The significance of difference in means shape between samples was investigated by performing two nonparametric tests on the size-standardized data using the TwoGroup6h software (Sheets 2005). The first test performs bootstrap resampling of specimens to determine whether the partial Procrustes distance between the mean forms of two samples significantly differs from zero (for a methodological summary see Webster & Sheets 2010; and Webster 2011a for an applied example). The second nonparametric test investigates between-sample differences in mean shape using a bootstrap-based approach utilizing Goodall's F-test (Goodall 1991; Dryden & Mardia 1998) of Procrustes distance between sample means as the test statistic (summarized in Webster & Sheets 2010). The observed F-value is compared to the range of F-values obtained by randomly assigning specimens to samples (1600 replicates). Results of two parametric tests of the shape data (Hotelling's T² test, and Goodall's F-test; see Webster & Sheets 2010 and references therein for methodological details) were entirely consistent with those of the nonparametric tests, and are not presented herein.

Variation in shape is quantified as the average partial Procrustes distance of specimens away from the sample mean. Bootstrap resampling (with replacement, 1600 replicates) of each sample permits calculation of the 95% confidence limits on each sample variance (for a methodological summary see Webster & Sheets 2010; for
Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*

**Systematic palaeontology**

Order **Redlichiida** Richter, 1932  
Suborder **Olenellina** Walcott, 1890  
Superfamily **Olenelloidea** Walcott, 1890  
Family **Olenellidae** Walcott, 1890  
Genus **Olenellus** Hall, 1861  
**Olenellus gilberti** Meek in White, 1874  
(Figs 6–15, 19–21, 25–29, 31–33, 36)

**Synonymy, type material and occurrence.** See Supplemental Data.

**Description.** (Mature morphology, late phase 5 of cephalic development, sagittal cephalic length > 9.3 mm). Cephalon semicircular in outline; proximal portion of posterior cephalic margin orientated weakly posteriorly by up to 10° relative to a transverse line when traced abaxially (Fig. 4A), distal portion flexing anteriorly by approximately 20° to 45° relative to proximal portion (Fig. 4B) at rounded adgenal angle located approximately 60% of distance from axial furrow to base of genal spine (Fig. 4C). Greatest observed cephalic length estimated to exceed 64 mm (sag.; Fig. 6D). Genal spine slender, base transversely opposite posterior (Fig. 7A), middle, or anterior portion of lateral margins of LO or SO (Figs 7B, 4D); length approximately two-thirds cephalic length (sag.). Distance (tr.) between genal spine bases 140% to 190% of cephalic length (sag.; Fig. 4E). Intergenal spine reduced to tiny node located on posterior cephalic border between adgenal angle and base of genal spine or absent. Cephalic border well defined around entire cephalon by distinct border furrow; flattened dorsally; width of anterior border opposite junction of ocular lobes with LA approximately 8% length (exsag.) of glabella (Fig. 4F). Preglabellar field short, sagittal length approximately equal to or less than that of anterior cephalic border, decreasing in proportional length through late phase 5 of cephalic development, very short to virtually absent on some large specimens (Fig. 6A) although two very large specimens (Fig. 6C, D) bear a preglabellar field approximately as long as anterior border. Plectron present (Figs 7C, E, 8E) except when preglabellar field is extremely short. Glabella hourglass-shaped, weakly constricted at S1; 85% to 93% of cephalic length (sag.; increasing slightly through late phase 5 of cephalic development; Fig. 5A). Maximum width of LA approximately 110% basal glabellar width (tr.; Fig. 5B). Posterior margin of glabella very weakly convex posteriorly. SO deep only abaxially, abaxial end slightly anterior to or more or less transversely opposite (Fig. 11A, C, G) adaxial end. LO subquadrate to subtrapezoidal, slightly narrowing anteriorly, length (exsag.) 12% to 17% of glabellar length (sag.; Fig. 5C). S1 deepest abaxially, approximately parallel to SO. L1 subtrapezoidal, slightly narrowing anteriorly; length (exsag.) 13% to 19% of glabellar length (sag.; Fig. 5D). S2 deepest in slot position, isolated from axial furrow, abaxial end slightly anterior to adaxial end. L2 and L3 merged distally, widening (tr.) anteriorly until contact with ocular lobes. S3 deepest in slot position, isolated from axial furrow, orientated anterolaterally away from axis until contact with ocular lobes. LA subcircular in outline, 77% to 120% as long (sag.) as wide (tr.), approximately 44% to 52% of glabellar length (sag.), separated from extraocular area by a sharp break in slope, weakly convex dorsally and not prominently inflated relative to extraocular area (although precise dorsal convexity and degree of inflation is uncertain due to compaction); widest point at contact with anterior margin of ocular lobes. Tiny axial node on posterior margin of LO. Ocular lobes divergent from exsagittal axis by up to 10° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of adaxial margin of ocular lobe with abaxial margin of L3; Fig. 5E), crescentic; posterior tip transversely opposite anterior half of lateral margin of LO (Fig. 7C, E), SO (Fig. 7D), or posteriormost L1 (Fig. 6B–D), typically more anteriorly located on larger cephalon (Fig. 5F); flat-topped dorsally. Very shallow ocular furrow sometimes developed; when present deepest anteriorly, inner band slightly wider (tr.) than outer band (Fig. 7A, C). Interocular area typically flat-topped (Fig. 7C), sometimes gently dorsally arched (Figs 7F, 8E, 11B) in transverse section, sometimes sloping down adaxially from ocular lobes to axial furrow (Fig. 7E), 68% to 119% as wide (tr.) as ocular lobes and 20% to 40% width (tr.) of extraocular area opposite S1. Extraocular genal caeca often present (Figs 7, 8); genal ridge (Figs 7F, 11G) and posterior ocular line (Figs 8D, 11D) sometimes present; intergenicual ridge (Fig. 8B) and anterior ocular line (Fig. 8C) very rarely developed. Berillon markings sometimes developed on LO (Figs 9B, D, 11F), rarely extends anteriorly on glabellar axis to LA (Fig. 9A) and very rarely ocular lobes (Fig. 9A). Terrace lines on dorsal surface of anterior cephalic border (sometimes grading laterally into wavy pattern; Fig. 9A), cephalic doublure (Figs 9C, 11C, E, G), and ventral surface of genal spines (Figs 9C, 11G).

Rostral plate narrower (sag.) than anterior and lateral cephalic border, crescent-shaped with axial ends curving to point slightly inwards in plan view; weakly convex ventrally in cross section (Figs 10A–C, 11D, 12B).

Mature hypostome (Fig. 8A, 10C–G, 14B) moderately convex (tr.), weakly convex (sag.), subcircular in outline. Anterior lobe of middle body subcircular, occupies approximately 85% of sagittal length of hypostome; anterior margin broadly curved; extends laterally onto broad, triangular anterior wings, tips of which are located slightly

**applied examples see Hopkins & Webster (2009) and Webster (2011a).** Shape variation was quantified on size-standardized data (above) using the DisparityBox software (Sheets 2007b).
posterior to hypostomal midlength. Posterior lobe of middle body very narrow, < 10% of hypostome length (sag.), transversely crescentic in outline, widest anteriorly, poorly distinguished from anterior lobe over sagittal axis. Maculae relatively deep. Anterior border narrow, sagittal width approximately 2% of hypostome length; defined by shallow furrow that broadens and deepens abaxially. Lateral and posterior border narrow, < 4% of hypostome length sagittally, weakly defined by shallow furrow. Five (?) pairs of very small, blunt spines/nubbins/swellings project posterolaterally from margin of lateral border; posterior border more or less straight (tr.) and without

Figure 4. Bivariate scatterplots depicting variation in various aspects of cephalic morphology amongst morphologically mature *Olenellus gilberti*, as summarized by traditional morphometric data. All variables plotted against sagittal cephalic length (mm). All data from cephalia in late phase 5 of development (> 9.3 mm in sagittal length) preserved as internal moulds from the Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945). A, orientation of the posterior cephalic margin (PCM) from the axial furrow to the adgenal angle (measured as the angle posterior to a transverse line); B, strength of the adgenal angle; C, location of the adgenal angle along the posterior cephalic margin (measured as the proportional distance of the adgenal angle along the posterior cephalic margin when traced from the axial furrow to the base of the genal spine); D, proportional anterior advancement of the genal spine bases, measured as the ratio of the exsagittal distance between the posterior limit of the sagittal axis and the base of the genal spine (GS Advancement) to sagittal cephalic length (CL); E, proportional width of the cephalon, measured as the ratio of transverse distance between the genal spine bases (GS Separation) to sagittal cephalic length (CL); F, proportional width of the anterior cephalic border, quantified as the ratio of the border width (measured anterior to the contact of the ocular lobes with LA) to sagittal glabellar length (GL).
Prominent, transversely ovate swelling developed at contact between posterior and lateral border, projects inwards into posterior lobe of middle body (Fig. 10D, E), rather more subdued on larger hypostomes (Fig. 10F, G). Ornament of concentric Bertillon markings on anterior lobe of middle body (Fig. 10E).

Prothorax of 14 segments; width (tr.) of axis typically 90% (range 76% to 100%) width (tr.) of inner pleural region on T1, gently tapering posteriorly. Axial node consistently present on posterior prothoracic segments from at least T11 (sometimes T6; Figs 11F, 13D) to T14, increasing in size posteriorly from axial swellings or small

Figure 5. Bivariate scatterplots depicting variation in various aspects of cephalic morphology amongst morphologically mature *Olenellus gilberti*, as summarized by traditional morphometric data. All variables plotted against sagittal cephalic length (mm). All data from cephalae in late phase 5 of development (> 9.3 mm in sagittal length) preserved as internal moulds from the Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945). A, proportional length of the glabella (GL, measured as sagittal length) relative to sagittal cephalic length (CL); B, proportional width of LA (measured as the maximal transverse width) relative to basal glabellar width (BG, measured as a transverse distance across the posterior margin of LO); C, proportional length of LO (exsagittal) relative to sagittal glabellar length (GL); D, proportional length of L1 (exsagittal) relative to sagittal glabellar length (GL); E, angle of divergence of the ocular lobe (OL) from the (ex)sagittal axis, measured as the angle between an exsagittal axis and a line drawn from the posterior tip of the ocular lobe to the contact of the adaxial margin of the ocular lobe with the abaxial margin of L3; F, proportional length of the ocular lobe (measured as a straight line from the point where the abaxial surface contacts LA to the posterior tip of the ocular lobe) relative to sagittal cephalic length (CL).
nodes to axial spinelets; axial node variably present (Figs 9B, 11F, 13B, C) or absent (Fig. 11B–D) on T1 and T2; axial structure not developed on T3 to T5. Inner pleural regions of T1 and T2 transverse, parallel-sided (those of T1 sometimes slightly tapering distally), with straight margins; pleural spines of T1 and T2 typically slender, divergent, sentate to weakly falcate, pleural spine of T2 slightly longer than that of T1. T3 macropleural; pleural spine macrospinous with posterior tip located transversely opposite axial ring of at least T11 (Figs 13A, 14A), sometimes extending beyond entire trunk (Figs 11D, 12B, 13B). Inner pleural region of T4 transverse, slightly tapering distally, with slightly curved anterior margin to accommodate distal expansion of T3; inner pleural

Figure 6. Largest morphologically mature specimens of *Olenellus gilberti* examined during the course of the present study (in late phase 5 of cephalic development). A, partially disarticulated specimen showing cephalon, slightly displaced hypostome, and T1 to T15 (T3 isolated off to left and rotated 90° clockwise), internal mould, UCR 9945.89, ×1; B, cephalon, internal mould, FMNH PE58384, ×0.9; C, cephalon and T1 to T6, latex cast of external mould, FMNH PE58385, ×0.9; D, cephalon and T1 to T15, external mould, FMNH PE58386, ×0.75. All in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Figure 7. Morphologically mature cephalas of *Olenellus gilberti* in late phase 5 of development. A, CMC P2303a, ×2; B, CMNH P1273, ×4; C, CMNH P1271, ×4; D, FMNH PE58387, ×2; E, CMC P2306c, ×4; F, FMNH PE58388, ×3. All internal moulds in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
regions of T5 to T7 or T8 transverse, parallel-sided, with straight margins; those of more posterior prothoracic segments increasingly divergent to pendent, with increasingly curved margins. Pleural spines of T4 and T5 slender, divergent, sentate to weakly falcate; those of T6 to T14 falcate, progressively increasing in length down the prothorax to T12 then proportionally decreasing in length on T13 and T14, transitioning from divergent to pendent to sometimes slightly convergent (Fig. 15B) on T9 to 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 and T5 or T6 to T14, rarely also T4 (Figs 6A, D, 10A, D), very rarely extending onto base of pleural spine of T2 (Figs 6A, 11C) or T1 and T2 (Figs 6D, 11B). Bertillon markings sometimes evident on outer margin and rarely ventral surface of pleural spine of T1, T2, and/or T3 (Figs 6A, 11D). Bertillon markings or terrace lines sometimes evident on pleural spines of more posterior segments (Fig. 9F). Bertillon markings sometimes developed on axis of T1, T2, T3, T4, and/or T6 (Figs 9B, 12C).

Some specimens show anomalously small pleural spines on one side of particular segments, perhaps indicative of injury or malformation (left side of T8 on Fig. 11D, right side of T4 and T5 on Fig. 12D; also Palmer, 1998, fig. 9.2, 9.4).

Opisthothorax of two (Figs 14A, 15A), three (Figs 14C, D, 15C, D), or sometimes possibly four (Palmer 1998, p. 667) segments. Long, slender, axial spine on T15 (length 85% to 95% as long as entire prothorax (sag.); Figs 11E, 12B), base as wide as T15 axis (Fig. 15B, C); no axial structures developed on more posterior segments. Axes of all segments poorly defined by break in slope; axial furrows not incised. Transversely orientated, crescent-shaped furrow crosses axis on at least some specimens (Fig. 15A, D); this might represent an articulating furrow or a taphonomic artefact. Inner pleural regions much narrower than axes (tr.); margins curved, converge into short, weakly divergent to pendent, sentate pleural spines. Pleural furrows not evident. Axial spine of T15 sometimes bears granular ornament (Figs 9E, 12A) and Bertillon markings at the spine base (Fig. 6A).

Figure 8. Morphologically mature specimens of Olenellus gilberti in late phase 5 of cephalic development. A, cephalon, hypostome in life position, and prothorax, latex cast of internal mould, FMNH PES8390, ×3 (see also Fig. 14B); B, cephalon, internal mould, CMC P2327, ×2; C, cephalon, internal mould, CMC P2355, ×2; D, cephalon, internal mould, UCR 9945.76, ×3; E, cephalon and prothorax, internal mould, UCR 9945.79, ×3 (see also Fig. 11B). All in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Pygidium tiny (Figs 14, 15), length approximately 7% to 9% of cephalic length (sag.); subquadrate to subcircular; posterior margin smoothly convex posteriorly, without median notch. Axis very weakly defined by break in slope, triangular, tapering posteriorly to blunt point, terminating well anterior to posterior pygidial margin, not segmented (Fig. 15C, D). Pleural field slopes down to pygidial margin, pygidial border not defined.

Ontogeny

Instar recognition. Five distinct clusters of *Olenellus gilberti* cephalas can be recognized based on size-clustering evident in plots of the relationship between the transverse distance between the bases of the intergenal spines and sagittal cephalic length (Fig. 16A, B). These size-clusters are interpreted to be putative instars. Growth ratios (Dyar’s coefficients) between successive putative instars average 1.20 for cephalic length (instar 1 to 2 = 1.23; instar 2 to 3 = 1.19; instar 3 to 4 = 1.21; instar 4 to 5 = 1.17). Growth ratios between successive putative instars average 1.41 for the transverse distance between the bases of the intergenal spines (instar 1 to 2 = 1.52; instar 2 to 3 = 1.36; instar 3 to 4 = 1.37; instar 4 to 5 = 1.40). The average per-moult growth increment (AGI), calculated as the average log-size increment between successive instars (Fusco et al. 2012) is 0.183 for sagittal cephalic length and 0.347 for the transverse distance between the bases of the intergenal spines. These growth coefficients are biologically reasonable when compared to values for other trilobites (Palmer 1957; Hunt & Chapman 2001; Fusco et al. 2004, 2012; Webster 2007b).

Statistical support for the existence of these size-clusters (instars) was investigated using the maximum likelihood analysis of mixture models approach of Hunt & Chapman (2001). This approach assumes that the data represent a sampling of (an unknown number of) underlying normal distributions, and uses maximum likelihood to determine the number of normal distributions (and their location and dispersion parameters) that best fit the data (Hunt & Chapman 2001). In the present application, each normal distribution is hypothesized to represent an instar. The mixture model analysis was conducted using FMCBox (Sheets 2003b), and was performed on data...
Figure 10. Morphologically mature hypostomes and rostral plates of Olenellus gilberti. A, specimen in moult configuration, with hypostome and rostral plate inverted and swung into posterior orientation relative to cephalon, internal mould, FMNH PE58397; ×2; B, specimen in unusual sclerite configuration, with cephalon and slightly displaced hypostome plus rostral plate isolated from T1; T2 to T8 are inverted, rotated by 90°, and displaced anterolaterally relative to these sclerites; and more posterior prothoracic segments are displaced and rotated by 90° relative to those; specimen preserved in calcite halo, UCR 9945.129, ×2; C, isolated hypostome and rostral plate, internal mould, ventral view, FMNH PE58398, ×1.5; D, hypostome, internal mould, ventral view, FMNH PE58399, ×7; E, hypostome, internal mould, ventral view, FMNH PE58401, ×4; F, hypostome, internal mould, ventral view, FMNH PE58402, ×4; G, hypostome, internal mould, ventral view, FMNH PE58403, ×3. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
from only small cephalae (i.e. those falling within the size range over which the five putative instars have been identified). The sample size available for this analysis far exceeds that in previous studies of olenelloid instars (Palmer 1957; Webster 2007b). Size-clusters are evident in the size distributions of sagittal cephalic length (Fig. 16C) and the transverse distance between the bases of the intergenal spines (Fig. 16D), but are most obvious on a bivariate plot of both traits (Fig. 16B). The mixture model analysis was therefore conducted on specimen scores along the first principal component of the (log-transformed) bivariate data, equivalent to the scores on the major axis of the data and assumed to represent the ‘ontogenetic axis’ (see Hunt & Chapman 2001, p. 474 for
Figure 12. Morphologically mature specimens of *Olenellus gilberti* (late phase 5 of cephalic development). **A**, cephalon and complete prothorax plus T15, internal mould, FMNH PE58396, ×3 (see also Fig. 9E); **B**, cephalon and complete prothorax plus T15, rostral plate almost in life position, internal mould, FMNH PE58407, ×3; **C**, cephalon and complete prothorax plus T15, latex cast of external mould, FMNH PE58408, ×1.5; **D**, cephalon and almost complete prothorax, latex cast of external mould, FMNH PE58409, ×1.5. All dorsal views. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Figure 13. Morphologically mature specimens of *Olenellus gilberti* (late phase 5 of cephalic development). A, cephalon and complete prothorax plus T15, FMNH PE58410, ×1.5; B, cephalon and complete prothorax plus T15, FMNH PE58411, ×3; C, cephalon and complete prothorax plus T15, FMNH PE58412, ×1.5; D, cephalon and complete prothorax plus T15, FMNH PE58413, ×3. All latex casts of external moulds in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Figure 14. Morphologically mature complete dorsal exoskeletons of *Olenellus gilberti* (late phase 5 of cephalic development). A, internal mould, UCR 9945.43, ×2 (see also Fig. 15A); B, internal mould, FMNH PE58390, ×2 (see also Figs 8A, 15B); C, latex cast of external mould, FMNH PE58417, ×1.5 (see also Fig. 15C); D, latex cast of external mould, FMNH PE58418, ×2 (see also Fig. 15D). All in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
further justification of this approach. AIC-compact (AIC-C) scores and weights strongly support the presence of size-clusters with normal distributions within the data (Table 1). However, the strongest support is for the presence of four such distributions (Table 1): the method combines putative instars 3, 4, and 5 into two groups, both with much higher variance than the other groups (Table 2). (The method also supported four distributions when the scores were based on PCA of the raw [not log-transformed] variables, essentially combining putative instars 3 and 4 into a single group with markedly higher variance than the other groups [data not shown]). It is therefore possible that the three largest (in terms of cephalic length) visually determined size-clusters (Fig. 16B) are erroneously identified, and in fact represent just two size-clusters. However, it is more likely that the mixture model analysis fails to identify the five size groupings because the data fail to meet the underlying assumption of the analysis, namely that each of the distributions is normal. In the present case, PC1 scores for all putative instars are

Figure 15. Details of opisthothorax and pygidium of morphologically mature Olenellus gilberti (late phase 5 of cephalic development). A, internal mould, UCR 9945.43, ×6; B, internal mould, FMNH PE58390, ×10 (see also Fig. 8A); C, latex cast of external mould, FMNH PE58417, ×10; D, latex cast of external mould, FMNH PE58418, ×10. All in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Figure 16. Recognition of and size variance within instars of *Olenellus gilberti*. A, ratio of transverse distance between intergenal spine bases to sagittal cephalic length plotted against sagittal cephalic length for all silicified specimens \( n = 524 \). Plot has been fitted with a distance weighted least squares regression function (LOWESS) to illustrate continuously increasing ratio through ontogeny. Note that small specimens fall into five size clusters (see B). B, five instars (numbered) revealed by size-clustering in a plot of transverse distance between adaxial margins of intergenal spine bases against sagittal cephalic length for smallest specimens shown in A \( n = 316 \). C, histogram of sagittal cephalic length for smallest silicified specimens \( n = 342 \). The five peaks (numbered) correspond to the average value for each of the five instars. D, histogram of transverse distance between intergenal spine bases for smallest silicified specimens \( n = 326 \). The five peaks (numbered) correspond to the average value for each of the five instars. E, variance in log-transformed cephalic length over instars 1 to 5. F, variance in log-transformed transverse distance between intergenal spine bases over instars 1 to 5. All specimens from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*  

Table 1. Results of mixture model analysis performed on specimen scores along the first principal component of the log-transformed bivariate data shown in Figure 16B. See text for details and interpretation. Statistics of the strongly supported four-distribution model are provided in Table 2.

| Number of normal distributions | AIC-C score | AIC-C deviance | AIC-C weights |
|--------------------------------|-------------|----------------|---------------|
| 1                              | 899.785     | 120.154        | 0             |
| 2                              | 847.216     | 67.585         | 0             |
| 3                              | 853.533     | 73.902         | 0             |
| 4                              | 779.631     | 0.000          | 1             |
| 5                              | 928.514     | 148.883        | 0             |
| 6                              | 942.520     | 162.889        | 0             |

Table 2. Statistics of the four normal distributions, as strongly supported by the mixture model analysis (Table 1). See text for details and interpretation.

| Distribution | Weight | Mean  | STD  |
|--------------|--------|-------|------|
| 1            | 0.129  | -1.522| 0.184|
| 2            | 0.325  | -0.600| 0.155|
| 3            | 0.307  | 0.191 | 0.532|
| 4            | 0.239  | 1.349 | 0.370|

Abbreviation: STD, standard deviation.

platykurtic, with those of putative instar 5 being significantly so (Anscombe–Glynn test, kurtosis = 1.988, z = -2.2557, p = 0.024). (Similar non-normality is seen in cephalic length data: values for instar 2 are significantly leptokurtic and for instar 5 are significantly platykurtic [data not shown].) Additional support for the distinctness of instars 4 and 5 as recognized on the bivariate plot comes from the fact that instar 5 specimens bear an incipient genal spine that is absent on instar 4 cephalon. These observations support the recognition of five instars within the data, the largest of which represents the first instar in phase 3 of cephalic development. Unlike in *Nephrolenellus* species, *O. gilberti* shows no change in the sign of the rate of transverse elongation of the posterior cephalic margin relative to the rate of increase in cephalic length amongst these five instars (compare Fig. 16A to Webster 2007b, fig. 2.1, 2.2). The first four instars of *O. gilberti* are therefore recognizable only as being in 'pre-phase 3' of cephalic development (see above and discussion below).

Description of ontogeny

Pre-phase 3. Observed cephalic lengths range from 0.61 mm to 1.08 mm, comprising four instars. The dearth of landmarks on cephalon in pre-phase 3 of development precludes geometric morphometric analysis of shape change during this portion of development. Quantitative analysis is therefore restricted to simple length and angular measures (Figs 16, 17, 18).

Initial morphology (instar 1) (Fig. 19A–F). Average sagittal cephalic length 0.61 mm. Cephalon horseshoe-shaped to subcircular in outline; maximum cephalic width (tr.) approximately 111% (range 104% to 117%) of sag. cephalic length. Posterior cephalic margin between bases of intergenal spines roughly transverse or slightly anterolaterally orientated when traced abaxially. Intergenal spines cylindrical in cross section, posteroventrally orientated at approximately 70° relative to plane of cephalic border (Fig. 19B, E), proximal portions very slightly convergent, distal portions parallel to exsag. axis or slightly divergent; length approximately 60% of cephalic length (sag.); distance (tr.) between adaxial margins of intergenal spine bases approximately 31% of cephalic length (sag.; Fig. 16A). Anterior border gently rounded dorsally, extends around lateral cephalic margin until contact with ocular lobes; sagittal length approximately 6% of cephalic length (sag.). Glabella, ocular lobes and interocular area together form dorsally convex (sag. and tr.) vaulted region that slopes steeply anteriorly into more flattened frontal area; length (sag.) of vaulted region approximately 80% cephalic length (sag.), highest point slightly posterior to cephalic midlength (sag.). Glabella barely defined by extremely shallow axial furrows, most clearly defined posteriorly; oval in outline, widest (tr.) at midlength (sag.); anterior portion forms subtle depression between anterior ends of ocular lobes; glabellar lobes not defined. Posterior margin of glabella weakly convex posteriorly, occupying much of distance between bases of intergenal spines, slightly elevated above bases of intergenal spines such that posterior cephalic margin slopes down when traced abaxially (Fig. 19B). Ocular lobes crescent-shaped in dorsal view, differentiated from interocular area by very shallow furrow; strongly divergent proximally, bending to run almost parallel with exsagittal axis, posterior portions slightly convergent; posterior tips more widely separated than anterior tips; broadly convex in cross-section (tr.), dorsal summit lower than highest points of interocular area and glabella. Ocular lobes contact and run confluent with lateral cephalic margin at and posterior to widest (tr.) point of cephalon. Posterior tips of ocular lobes located transversely opposite point approximately 17% along sagittal axis (measured from posterior end); merge into posterior ocular line that extends to abaxial margin of intergenal spines. Interocular area dorsally arched (tr. and exsag.), sloping down (tr.) from glabella to ocular lobes; interocular furrows not developed. Intergenal ridge runs from posterior portion of interocular area (presumably as pleural extension of L1) onto base of intergenal spines. Doublure runs around entire ventral margin, widest below lateral cephalic margins (Fig. 19F).
Figure 17. Bivariate scatterplots depicting variation in various aspects of cephalic morphology during the ontogeny of *Olenellus gilberti*, as summarized by traditional morphometric data. All variables plotted against sagittal cephalic length (mm). All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963). Symbols refer to phases of cephalic development: Δ, pre-phase 3; +, phase 3; ×, phase 4; ○, early phase 5; downward-pointing triangles indicate specimens of ambiguous phase assignment (i.e. either phase 3 or phase 4; either phase 4 or early phase 5). 

A, proportional width of the cephalon, measured as the ratio of transverse distance between the genal spine bases (GS Separation) to sagittal cephalic length (CL); B, proportional maximum transverse width across LA relative to transverse width across S3; C, proportional transverse width across S3 relative to transverse width across S1; D, proportional transverse width across S3 relative to transverse width across base of glabella (BG); E, proportional length of the ocular lobe (measured as a straight line from the point where the abaxial surface contacts LA to the posterior tip of the ocular lobe) relative to sagittal cephalic length (CL); F, angle of divergence of the ocular lobe (OL) from the (ex)sagittal axis, measured as the angle between an ex-sagittal axis and a line drawn from the posterior tip of the ocular lobe to the contact of the adaxial margin of the ocular lobe with the abaxial margin of L3.
Figure 18. Bivariate scatterplots depicting variation in various aspects of cephalic morphology during the ontogeny of *Olenellus gilberti*, as summarized by traditional morphometric data. All variables plotted against sagittal cephalic length (mm). All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963). Symbols refer to phases of cephalic development: Δ, pre-phase 3; +, phase 3; ×, phase 4; ⨝, early phase 5; downward-pointing triangles indicate specimens of ambiguous phase assignment (i.e. either phase 3 or phase 4; either phase 4 or early phase 5). A, proportional length of the glabella (GL, measured as sagittal length) relative to sagittal cephalic length (CL); B, proportional width of the anterior cephalic border, quantified as the ratio of the border width (measured anterior to the contact of the ocular lobes with LA) to sagittal cephalic length (CL); C, proportional maximum transverse width across LA relative to transverse width across base of glabella (BG); D, proportional exsagittal length of L3 relative to sagittal glabellar length (GL); E, proportional exsagittal length of L2 relative to sagittal glabellar length (GL).
Instar 2 (Fig. 19G–L). Average sagittal cephalic length 0.75 mm. Relative to the first instar, the posterior cephalic margin is longer (tr.), such that the distance (tr.) between the adaxial margins of intergenal spine bases is approximately 38% of cephalic length (sag.; Fig. 16A). The cephalic border extends around the entire lateral cephalic margin, terminating against the posterior ocular line at the abaxial margin of the base of the intergenal
spines; the outer margin of the ocular lobe slopes into the lateral cephalic border furrow. The cephalon is less prominently dorsally vaulted (sag. and tr.). The proximal portion of the intergenal spine is orientated posteroventrally at a less steep angle (approximately 40°) relative to the plane of cephalic border (Fig. 19H, J), and the spine flexes distally into an even less steeply dipping orientation. The intergenal spines are also typically proportionally longer (up to 75% of sagittal cephalic length), although their delicate tips are rarely preserved. The second instar also bears a transversely orientated SO furrow, defining a narrow LO that occupies slightly less than 10% of the cephalic length (sag.). The adaxial limit of the intergenal ridge lies transversely just anterior to SO. The posterior tips of the ocular lobes are located slightly more anteriorly (transversely opposite a point approximately 20% along the sagittal axis [measured from posterior end]).

**Instar 3** (Fig. 19M–P). Average sagittal cephalic length 0.89 mm. Two differences between the second and third instar are extensions of differences between the first and second instar. Firstly, relative to the second instar, the posterior cephalic margin of the third instar is longer (tr.), such that the distance (tr.) between the adaxial margins of intergenal spine bases is approximately 43% of cephalic length (sag.; Fig. 16A). Secondly, the proximal portion of the intergenal spine on the third instar is orientated posteroventrally at a less steep angle (approximately 35°) relative to the plane of cephalic border (Fig. 19O). However, the intergenal spines of the third instar are typically proportionally shorter (slightly less than 66% of sagittal cephalic length) than those of the second instar.

Glabellar furrows are not expressed on the third instar, but the axial furrow contains subtle pit-like depressions located at the anterolateral and posterolateral corners of glabellar lobes L1, L2, and L3 (Fig. 19M, N). LO occupies 10% to 13% of the cephalic length (sag.), with a posteriorly convex posterior margin and a sagittal swelling (axial node?); the lateral margins of LO are poorly differentiated from the posterior cephalic border, but it appears to be approximately as wide or slightly narrower (tr.) than L1. L1, L2 and L3 each occupy approximately 14% to 18% of cephalic length and are slightly trapezoidal in outline (narrower anteriorly), so that the glabella slightly tapers in width (tr.) anteriorly from SO to S3. LA remains poorly defined as a subtle depression between the anterior ends of the ocular lobes; anteriorly, LA slopes steeply into the preglabellar field and is not defined by axial furrows. The intergenal ridge is clearly a pleural extension of L1. The posterior tips of the crescentic ocular lobes are located transversely opposite the midlength or posterior half of L1. The doublure is much narrower along the posterior cephalic margin than around the rest of the cephalon (Fig. 19P).

**Instar 4** (Fig. 19Q–V). Average sagittal cephalic length 1.08 mm. The two ontogenetic trends of widening of the posterior cephalic margin between the bases of the intergenal spines and of rotation of the intergenal spines into a less steeply ventrally dipping orientation continue from the third instar into the fourth instar. On the fourth instar the distance (tr.) between the adaxial margins of intergenal spine bases averages 49% of cephalic length (sag.; Fig. 16A) and the proximal portion of the intergenal spine dips ventrally at a mean of 29° relative to the plane of cephalic border (Fig. 19R). The intergenal spines are typically approximately two-thirds as long as the sagittal axis of the cephalon (although the spine tips are rarely preserved and this might be an underestimate), and each bears a very narrow slit-like opening that runs along its ventral side (Fig. 19U, V; the presence of absence of these slits on earlier instars is unclear due to the relatively coarse preservation). The glabella occupies approximately 75% to 81% of cephalic length (sag.) and is essentially unchanged from its condition on the third instar except that LA is relatively more inflated: it is pear-shaped in plan view (broadly rounded anteriorly, widest at the point of contact with the anterior tips of the ocular lobes, somewhat narrower between the ocular lobes) and clearly delimited from the preglabellar field by a break in slope; the summit of LA is slightly lower than the summit of the ocular lobes. The ocular lobes are separated from the lateral cephalic border by a very narrow (tr.), crescent-shaped extraocular area that extends posteriorly to the posterior ocular line (Fig. 19Q, S). The doublure narrows anteriorly from the lateral to the anterior margin, providing accommodation for a crescent-shaped rostral plate that extends around the anterior third of the ventral cephalic margin and widens across the sagittal axis (Fig. 19V). At least one terrace line runs around the doublure (Fig. 19U, V). One coarsely preserved anomalous specimen (Fig. 19T) exhibits intergenal spines that curve to the right and are approximately 40% longer than the sagittal axis of the cephalon. It is unclear whether the curvature of the spines on this specimen represents a developmental anomaly or a taphonomic artefact.

**Phase 3.** Observed sagittal cephalic lengths range from 1.27 mm to at least 2.03 mm (possibly 2.3 mm). Several silicified cephala ranging from 1.78 mm to 2.30 mm in sagittal length represent either late phase 3 or early phase 4 of development (downward-pointing triangles on Figs 17, 18), but precise phase assignment remains ambiguous due to their coarse, grainy preservation. This in turn leads to uncertainty regarding the maximum size of phase 3 cephalon.

**Initial morphology (instar 5)** (Fig. 20A–H). Average sagittal cephalic length 1.27 mm. Cephalon horseshoe-shaped in outline; maximum cephalic width (tr.) approximately 113% (range 104% to 119%) of sag. cephalic length. Posterior cephalic margin between bases of
Figure 20. Silicified morphologically immature cephalas of *Olenellus gilberti* in early phase 3 of development (instar 5 and beyond). A, B, instar 5, dorsal and ventral views, FMNH PE58429, ×30; C, D, instar 5, dorsal and ventral views, FMNH PE58430, ×30; E, F, instar 5, dorsal and left lateral views, FMNH PE58431, ×30; G, H, instar 5, dorsal and right lateral views, FMNH PE58432, ×28; I, J, post-instar 5, dorsal and left lateral views, FMNH PE58433, ×25; K–N, post-instar 5, dorsal, ventral, left lateral and anterior views, UCR 9963.107, ×25; O, post-instar 5, dorsal view, FMNH PE58434, ×25; P, post-instar 5, dorsal view, FMNH PE58435, ×25; Q, R, post-instar 5, dorsal and right lateral views, FMNH PE58436, ×22. All from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
intergenal spines slightly posterolaterally orientated and dips slightly downwards when traced abaxially. Intergenal spines cylindrical in cross section with very narrow slit-like opening running along ventral side (Fig. 20B), posteroventrally orientated at approximately 16° relative to plane of cephalic border (Fig. 20F, H), slightly divergent along their length; tips rarely preserved but spines approximately as long as cephalon (sag.) on some specimens (Fig. 20C, D); distance (tr.) between adaxial margins of intergenal spine bases averages 59% of cephalic length (sag.; Fig. 16A). Anterior border gently rounded dorsally, sagittal length approximately 9% of cephalic length (sag.; Fig. 18B); border extends around lateral cephalic margin to base of intergenal spines. Glabella widest (tr.) at SO, tapers slightly anteriorly to S3; approximately 77% cephalic length (sag.; Fig. 18A); weakly defined by shallow axial furrow that contains subtle pit-like depressions located at the anterolateral and posterolateral corners of glabellar lobes L1, L2 and L3. SO shallowly incised across entire glabella, straight, transverse; other glabellar furrows extremely weak or not expressed. LO subtrapezoidal, widening slightly (tr.) anteriorly; sagittal length approximately 10% to 13% of cephalic length (sag.); lateral margins poorly differentiated from posterior cephalic border; posterior margin convex posteriorly. L1, L2 and L3 each approximately 14% to 16% of cephalic length (sag.; Fig. 18D, E); each slightly trapezoidal in outline (narrower anteriorly). LA broadly rounded anteriorly, widest (tr.) at point of contact with anterior tips of ocular lobes, slightly narrower between ocular lobes; clearly delimited from almost flat preglabellar field by break in slope (Fig. 20F, H); summit slightly lower than summit of ocular lobes. Maximum width (tr.) of LA approximately equal to glabellar width at SO. Sagittal swelling (axial node?) on axis of LO. Ocular lobes crescent- to sausage-shaped in dorsal view, differentiated from interocular area by shallow furrow; strongly divergent proximally, bending to run almost parallel with exsagittal axis; posterior tips more widely separated than anterior tips and located transversely opposite posteriormost lateral margin of L1; broadly convex in cross section (tr.), rising steeply from extracocular area at sharp break in slope; dorsal summit slightly higher than highest points of interocular area and anterior portion of glabella. Interocular area very weakly dorsally arched (tr.), adaxial and abaxial ends more or less on same dorsal plane opposite lateral margins of L2; interocular furrows not visible. Weak intergenal ridge runs onto adaxial portion of intergenal spines; much weaker posterior ocular line extends to abaxial margin of intergenal spines. Very narrow (tr.), crescent-shaped extracocular area extends posteriorly to posterior ocular line. Genal spine represented as a tiny nubbin on the cephalic doublure, immediately outside and slightly ventral to abaxial margin of base of intergenal spine (Fig. 20B, D); barely visible in dorsal view (Fig. 20A, C, E, G).

Subsequent change. Considerable morphological change occurred during phase 3 of cephalic development (Figs 17, 18, 20, 21). The extracocular area continued to widen (tr.), with a corresponding elongation (tr.) of the posterior cephalic margin between the axial furrow and the base of the intergenal spine (compare Fig. 20A–G to Figs 20I–R, 21). The intergenal spine bases, which were initially located more or less directly behind (exsag.) the posterior tips of the ocular lobes (Fig. 20A–G), migrated to positions posterior to and well outside the abaxialmost points of the ocular lobes (Figs 20I–R, 21). The transverse distance between the genal spine bases also proportionally increased relative to sagittal cephalic length during phase 3 (Fig. 17A). The genal spines developed first from tiny nubbins clearly visible only in ventral view (instar 5; Fig. 20A–E, G) into short bud-like projections clearly visible in dorsal view (Fig. 20I–Q), and then progressively elongated into stout spines that are slightly longer than the sagittal length of LO on cephala in late phase 3 of development (Fig. 21D, K, N). The bases of the genal and intergenal spines became slightly separated by a short (tr.) elongation of the cephalic border (Fig. 21D, G, K, N). The genal spine bases are located slightly distal to and anterior to the intergenal spine bases, so that a strong intergenal angle is present (Fig. 21D, G, K, N). Some cephala in mid- to late phase 3 of development also possess a weak adgenal angle along the posterior cephalic margin approximately midway between the axial furrow and the base of the intergenal spine (Fig. 21D, N). The intergenal spines swung into an orientation that is coplanar with the cephalic margin (compare Fig. 20J, M, R to Fig. 21F, I, O) and proportionally shortened, being approximately two-thirds as long as the cephalon (sag.) by late phase 3 of development (Fig. 21N). A weak anterior arch is present on cephala in late phase 3 of development (Fig. 21E, H, L). Glabellar furrows became better defined; all are straight, transverse, and are incised across the entire glabella on cephala in late phase 3 of development (Fig. 21B–N). LO proportionally widened (tr.), especially posteriorly, so that the glabella tapers evenly from the posterior margin to L2 or S3 on late phase 3 cephala (Fig. 21B–N). LA continued to inflate dorsally, so that on late phase 3 cephala the summit of LA is as high as the summit of the ocular lobes (Fig. 21E, H, L). L3 proportionally widened (tr.), so that its anterolateral margins contact the inner margins of the ocular lobes on late phase 3 cephala (Fig. 21N). On cephala in late phase 3 of development, the transverse width of the glabella across S3 is approximately equal to the transverse width of LA where it meets the outer margins of the ocular lobes (Figs 17B, 21N), and the transverse width of the glabella across S3 is typically wider than the transverse width across S2 or S1 (Fig. 17C) and approximately as wide as the basal glabellar width (Fig. 17D). The ocular lobes proportionally slightly shortened relative to sagittal cephalic length.
(Fig. 17E) and became progressively less divergent from the exsagittal axis (measured as the angle between the exsagittal axis and a line from the posterior tip of the ocular lobe to the contact of the inner margin of the ocular lobe with the axial furrow; Fig. 17F). The visual surface is missing on some cephalas in late phase 3 of development (Fig. 21H, I), suggesting that the circumocular suture was functional at this stage. The posterior ocular line and intergenal ridge became greatly reduced in prominence (the latter may be absent) relative to ontogenetically younger cephalas. The axial node on LO became better defined (Fig. 21G, K, N).
One very grainily preserved silicified specimen (Fig. 21J) shows a trunk articulated with the cephalon. The trunk is triangular in outline, being widest anteriorly and tapering posteriorly to a point. The number of trunk segments cannot be determined due to the coarse preservation, but one segment close to the anterior of the trunk (presumably T3) bears straight, slightly divergent, macrospinous pleural spines that are approximately twice as long as the rest of the trunk.

Glabellar segmentation became well defined only relatively late during phase 3 of development. This restricts geometric morphometric analysis of glabellar shape variation to only the late portion of phase 3. There is minimal size variation amongst phase 3 cepha from which glabellar landmarks can be digitized, and the observed glabellar shape variation contains little to no ontogenetic signal (Figs 22B, G, 23B, G). Indeed, the pattern of glabellar shape change over this limited size range cannot be statistically distinguished from one of isometry (data not shown). However, a wider size range of phase 3 cepha can be included in a geometric morphometric analysis if landmarks relating to glabellar segmentation are excluded (Fig. 24A). This reduced landmark configuration permits visualization of the pattern of ontogenetic shape change within phase 3 (Fig. 24B). The proportional transverse elongation of the posterior cephalic margin between the axial furrow and the base of the intergenal spine is evident, as is the outward migration of the intergenal spine base relative to the posterior tip of the ocular lobe. The subtle proportional widening (tr.) of the posterior margin of LO can also be seen.

**Phase 4.** Observed cephalic lengths range from at least 1.88 mm (possibly 1.78 mm) to at least 3.29 mm (possibly 3.58 mm). Several silicified cepha ranging from 3.13 mm to 3.58 mm in sagittal length represent either late phase 4 or early phase 5 of development (downward-pointing triangles on Figs 17, 18), but precise phase assignment remains ambiguous due to their coarse, grainy preservation. This in turn leads to uncertainty regarding the maximum size of phase 4 cepha. The smallest size of phase 4 cepha remains uncertain for the same reason (see above).

**Initial morphology** (Fig. 25A–G). Cephalon semicircular in outline; proximal portion of posterior cephalic margin orientated very slightly posteriorly when traced abaxially, distal portion flexing into a roughly transverse orientation at weak adgenal angle located approximately midway between axial furrow and base of intergenal spine. Intergenal spines cylindrical in cross section with very narrow slit-like opening running along ventral side (Fig. 25B), more or less coplanar with cephalic border (Fig. 25D, G), divergent along their length; tips rarely preserved but spines at least slightly more than one-third as long as cephalon (sag.) on some specimens (Fig. 25A). Genal spines stout, slightly longer than the length of LO (sag.), base transversely opposite lateral margins of LO. Genal spine bases slightly distal to and anterior to base of intergenal spines, separated by short (tr.) border; strong intergenal angle present. Distance (tr.) between adaxial margins of genal spine bases averages 116% of cephalic length (sag.; Fig. 17A). Cephalic border well defined by distinct border furrow except at bases of intergenal spines where it is crossed by intergenal ridge/posterior ocular line; flattened dorsally; width of anterior border opposite junction of ocular lobes with LA approximately 9% sagittal cephalic length (Fig. 18B) and averaging almost 80% length (exsag.) of LO. Weak anterior arch present (Fig. 25C, F). Glabella weakly hourglass-shaped, slightly constricted at L2; approximately 78% of cephalic length (sag.; Fig. 18A), preglabellar field short (sagittal length approximately equal to or slightly longer than that of anterior cephalic border). Posterior margin of LO convex posteriorly. SO deepest abaxially, shallow over axis, roughly transverse or with abaxial end slightly anterior to adaxial end. LO subquadrate to subtrapezoidal, slightly narrowing anteriorly, length (exsag.) approximately 14% of glabellar length (sag.). S1 deepest abaxially, shallow over axis, approximately parallel to SO. L1 subtrapezoidal, slightly narrowing anteriorly; length (exsag.) approximately 17% of glabellar length (sag.). S2 deepest abaxially, shallow over axis, straight, transverse. L2 subquadrate to subtrapezoidal, slightly narrowing anteriorly. L3 subtrapezoidal, widening (tr.) anteriorly, anterolateral corners contact inner margins of ocular lobes; glabellar width (tr.) across S3 approximately 109% basal glabellar width (Fig. 17D). S3 deepest abaxially, shallow over axis, orientated weakly anterolaterally away from axis until contact with ocular lobes. LA approximately circular in plan view, widest at point of contact with outer margin of ocular lobes; width (tr.) across contact with outer margins of ocular lobes approximately 105% basal glabellar width (Fig. 18C); approximately 45% to 50% of glabellar length (sag.), separated from extraocular area by a sharp break in slope; dorsal summit as high or slightly higher than summit of ocular lobes (Fig. 25C, F). Axial node on LO. Ocular lobes divergent from exsagittal axis by approximately 18° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of inner margin of ocular lobe with abaxial margin of L3; Fig. 17F), crescentic, posterior tip transversely opposite midlength or anterior half of lateral margin of LO, flat-topped dorsally. Shallow ocular furrow often developed on at least anterior two-thirds of ocular lobe (Fig. 25A); when present, inner band slightly wider (tr.) than outer band. Intercocular area typically more or less flat-topped or sometimes weakly sloping down from the ocular lobes to the axial furrow in transverse section, approximately equal in width (tr.) to width (tr.) of ocular lobes and approximately 116% to 145% width (tr.) of extraocular area opposite S1. Weak
Figure 22. Results of geometric morphometric analyses of patterns of ontogenetic shape change of the glabella on morphologically immature cephalon of *Olenellus gilberti*. All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963; n = 84). Symbols refer to phases of cephalic development: +, phase 3; ×, phase 4; ⊙, early phase 5; downward-pointing triangles indicate specimens of ambiguous phase assignment (i.e. either phase 4 or early phase 5). A, location of eight landmarks around the periphery of the glabella used in the analyses. Paired homologous (non-sagittal) landmarks are shown only on the right side of the glabella for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, ‘rate’ of glabellar shape change as a function of glabella size. Amount of shape change through ontogeny is quantified as Procrustes distance of each specimen away from the consensus configuration of the three smallest specimens. Size is quantified as the natural logarithm of centroid size. C, scatterplot of data on plane defined by first two principal components (PC1 and PC2) following PCA of warp scores (reference form = mean of all configurations). D, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 74.5% of total variance). E, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 5.8% of total variance). F, thin-plate spline deformation grid showing shape variation when warp scores are regressed against the natural logarithm of centroid size (lnCS; reference form = consensus of three smallest specimens); this linear regression model represents a crude approximation of ontogenetic shape change; note the similarity to Fig. 22D. H, G, thin-plate spline deformation grid showing pattern of ontogenetic shape change during phase 3 of cephalic development. Obtained by regressing warp scores against lnCS for phase 3 specimens only (n = 18; reference form = consensus of three smallest specimens in phase 3). Growth is statistically indistinguishable from isometry. H, thin-plate spline deformation grid showing pattern of ontogenetic shape change during phase 4 of cephalic development. Obtained by regressing warp scores against lnCS for phase 4 specimens only (n = 59; reference form = consensus of three smallest specimens in phase 4). See text for details.
Figure 23. Results of geometric morphometric analyses of patterns of ontogenetic shape change of the glabella on morphologically immature cephalon of Olenellus gilberti. All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963; n = 116). Symbols refer to phases of cephalic development: +, phase 3; ×, phase 4; ○, early phase 5; downward-pointing triangles indicate specimens of ambiguous phase assignment (i.e. either phase 4 or early phase 5). A, location of seven landmarks around the periphery of the glabella used in the analyses. Paired homologous (non-sagittal) landmarks are shown only on the right side of the glabella for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, 'rate' of glabellar shape change as a function of glabella size. Amount of shape change through ontogeny is quantified as Procrustes distance of each specimen away from the consensus configuration of the three smallest specimens. Size is quantified as the natural logarithm of centroid size. Note decrease in 'rate' upon entry into early phase 5, as highlighted by LOWESS curve fitted to data. C, scatterplot of data on plane defined by first two principal components (PC1 and PC2) following PCA of warp scores (reference form = mean of all configurations). D, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 83.52% of total variance). E, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 4.7% of total variance). F, thin-plate spline deformation grid showing shape variation when warp scores are regressed against the natural logarithm of centroid size (lnCS; reference form = consensus of three smallest specimens); this linear regression model represents a crude approximation of ontogenetic shape change; note the similarity to D, H, I. G, thin-plate spline deformation grid showing pattern of ontogenetic shape change during phase 3 of cephalic development. Obtained by regressing warp scores against lnCS for phase 3 specimens only (n = 20; reference form = consensus of three smallest specimens in phase 3). Growth is statistically indistinguishable from isometry. H, thin-plate spline deformation grid showing pattern of ontogenetic shape change during phase 4 of cephalic development. Obtained by regressing warp scores against lnCS for phase 4 specimens only (n = 65; reference form = consensus of three smallest specimens in phase 4). I, thin-plate spline deformation grid showing pattern of ontogenetic shape change during early phase 5 of cephalic development. Obtained by regressing warp scores against lnCS for early phase 5 specimens only (n = 23; reference form = consensus of three smallest specimens in early phase 5). See text for details.
posterior ocular line and/or intergenal ridge present; crosses posterior cephalic border and runs onto intergenal spine. Doublure runs around entire ventral margin, widest below lateral cephalic margins, narrowest below posterior cephalic border and posterior margin of LO (Fig. 25B).

Subsequent change. Considerable morphological change occurred during phase 4 of cephalic development (Figs 17, 18, 25, 26). The extraocular area continued to proportionally widen (tr.), with a corresponding proportional elongation (tr.) of the posterior cephalic margin between the axial furrow and the base of the intergenal spine (Figs 25H–U, 26). The bases of the intergenal and genal spines also became proportionally more widely separated (Figs 25H–U, 26). The transverse distance between the genal spine bases averages almost 140% of sagittal cephalic length on late phase 4 cephala (Figs 17A, 26P). The intergenal angle decreased in strength and the adgenal angle increased in strength, so that the cephalic margin distal to the adgenal angle is orientated slightly anteriorly on cephala in late phase 4 of development (Fig. 26G–P). The intergenal spines proportionally reduced in size and are shorter than the length (exsag.) of LO on late phase 4 cephala (Fig. 26G–P). The genal spines concomitantly increased in length, being as long or longer than the intergenal spines by mid-phase 4 (Fig. 25K) and being more than half as long as the cephalon (sag.) on late phase 4 cephala (Fig. 26G, P). L3 proportionally widened (tr.), especially anteriorly, so that the degree of contact between its anterolateral margins and the inner margins of the ocular lobes increased and S3 became increasingly caret-shaped either side of the sagittal axis (Figs 25H–U, 26). On late phase 4 cephala the furrow along the line of contact between the anterolateral margin of L3 and the inner margin of the ocular lobe is very shallow, and S3 is deepest in the slot position (Fig. 26G–P). On cephala in late phase 4 of development, the transverse width of the glabella across S3 is approximately 110% to 130% of the basal glabellar width (Fig. 17D) and averages approximately 130% of the transverse width across S2 or S1 (Fig. 17C), so that the glabella is strongly constricted at L2. L3 and L2 also slightly proportionally shortened (exsag.) relative to glabellar length during phase 4 (Fig. 18D, E). LA proportionally widened (tr.; Fig. 18C), slightly elongated (sag.), and inflated, so that its summit is higher than the summit of the ocular lobes on late phase 4 cephala (Fig. 26). The rate of proportional widening (tr.) of L3 essentially matched that of LA, so that the maximum width of LA remained almost equal to glabellar width across S3 throughout phase 4 (Fig. 17B). The glabella slightly proportionally elongated (sag.), occupying up to 82% of sagittal cephalic length on late phase 4 cephala (Fig. 18A). The ocular lobes continued to proportionally slightly shorten relative to sagittal cephalic length (Fig. 17E) and to become progressively less divergent from the exsagittal axis (Fig. 17F). The posterior ocular line and intergenal ridge continued to reduce in prominence, and are sometimes absent altogether on late phase 4 cephala. A plectrum first becomes visible on mid- to late phase 4 cephala (Fig. 25K); it broadens (tr.) and is more prominent anteriorly where it merges into the anterior cephalic border. The anterior arch became more strongly developed during phase 4 (Figs 25, 26). The visual surface is often missing from cephala in mid- to late phase 4 of development (Figs 25S, T, V, W, 26H, I, N, O, Q, R). As inferred from the slit-like void bounded by the circumocular suture, the visual surface must have been long (spanning almost the entire length of the ocular lobe) but very limited in dorsoventral height. The lower margin of the visual surface was raised above the
Figure 25. Silicified morphologically immature cephalia of *Olenellus gilberti* in phase 4 of development. A–D, dorsal, ventral, anterior and left lateral views, UCR 9963.109, ×18; E–G, dorsal, anterior, and right lateral views, UCR 9963.112, ×18; H–J, dorsal, anterior and left lateral views, FMNH PES58442, ×17; K–M, dorsal, anterior and right lateral views, FMNH PES58443, ×17; N–P, dorsal, anterior and right lateral views, FMNH PES58444, ×17; Q–T, dorsal, ventral, anterior and left lateral views, UCR 9963.113, ×17; U–W, dorsal, anterior and right lateral views, FMNH PES58445, ×15. All from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
Figure 26. Silicified morphologically immature cephala of *Olenellus gilberti* in phase 4 of development. A–C, dorsal, anterior and left lateral views, FMNH PE58446, ×15; D–F, dorsal, anterior and right lateral views, FMNH PE58447, ×15; G–I, dorsal, anterior and left lateral views, FMNH PE58448, ×14; J–L, dorsal, anterior and right lateral views, FMNH PE58449, ×14; M–O, dorsal, anterior and left lateral views, FMNH PE58450, ×13; P–R, dorsal, anterior and right lateral views, FMNH PE58451, ×13. All from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
extraocular area by a prominent eye socle that was approximately equal in dorsoventral height to the visual surface itself (Figs 25, 26).

Geometric morphometric analysis of the glabella identifies the marked allometry of that structure during phase 4 of cephalic development (Figs 22B, H, 23B, H, 30B, F). The proportional widening (tr.) of L3, especially anteriorly, is evident, as is the proportional shortening (exsag.) of L3 and L2 (Figs 22H, 23H). Quantitative comparison of the pattern of cephalic shape change followed during phase 4 with that followed during phase 3 is limited to a landmark configuration that excludes landmarks relating to glabellar segmentation (see above; Fig. 24). The patterns of shape change are significantly different (at 90% confidence using vectors based on warp scores, Table 3; at 95% confidence using vectors based on Bookstein coordinates (between phase angle = 27.7°; bootstrapped range of angles within phase 3 = 15.9°; bootstrapped range of angles within phase 4 = 22.5°)). This result is robust against details of analytical method (choice of baseline for vectors based on Bookstein coordinates; choice of reference configuration for vectors based on warp scores) and against exclusion or assignment of the 12 specimens that may represent either phase 3 or phase 4 cephalon (data not presented). Quantitative comparison of the pattern of cephalic shape change followed during phase 4 with that followed during phase 5 is discussed below.

Cephalon in phase 4 of development preserved in a non-silicified state (from Ruin Wash) are very similar to their silicified equivalents (e.g. Fig. 27A–D), but low sample size of suitably preserved non-silicified specimens precludes quantitative comparison of shape between preservational modes. Trunk morphology during phase 4 of cephalic development is known from only one very poorly preserved specimen approximately 3.09 mm in sagittal cephalic length (FMNH PE57581, not illustrated). Few details can be gleaned from this specimen other than that it bears at least 12 thoracic segments and that T3 is macropleurally and macrospinously with the pleural furrow passing onto the base of its pleural spine.

Early phase 5. Observed cephalic lengths range from at least 3.57 mm (possibly 3.13 mm) to approximately 9.3 mm. The uncertainty regarding the minimum size of phase 5 cephalon results from ambiguous assignment of several grainily preserved cephalon to either phase 4 or phase 5 (see above).

Initial morphology (Fig. 28A–G). Cephalon semicircular in outline; proximal portion of posterior cephalic margin orientated more or less transversely or slightly posteriorly when traced abaxially, distal portion flexing anteriorly by approximately 19° to 25° relative to proximal portion at adgenal angle located approximately 60% of distance from axial furrow to base of genal spine. Genal spine slender, base transversely opposite midlength or anterior third of lateral margins of LO; length estimated to exceed one-half cephalic length (sag.). Distance (tr.) between adaxial margins of genal spine bases averages 140% of cephalic length (sag.; Fig. 17A). Intergenial spine located on posterior cephalic border between adgenal angle and base of genal spine; length less than half length (exsag.) of LO, cylindrical in cross section and closed ventrally (Fig. 28L). Cephalic border well defined around entire cephalon by distinct border furrow; flattened dorsally; width of anterior border opposite junction of ocular lobes with LA approximately 9% cephalic length (sag.; Fig. 18B) and three-quarters length (exsag.) of LO. Broad anterior arch present (Fig. 28B, F). Glabella hourglass-shaped, constricted at S1; approximately 80% to 82% of cephalic length (sag.; Fig. 18A), preglabellar field short,

| Sample 1 (preservation, N) | Sample 2 (preservation, N) | LM Config. | Ref. Form | Angle between samples | Within sample 1 | Within sample 2 | P-value |
|----------------------------|----------------------------|-------------|-----------|----------------------|----------------|----------------|--------|
| Ph 3 (S, 28)               | Ph 4 (S, 60)               | e8          | B         | 17.1                 | 11.9           | 17.4           | < 0.1  |
| Ph 4 (S, 65)               | e Ph 5 (S, 23)             | g7          | B         | 40.4                 | 24.8           | 39.3           | < 0.05 |
| Ph 4 (S, 65)               | e Ph 5 (NS, 108)           | g7          | B         | 43.5                 | 17             | 32.7           | < 0.05 |
| Ph 4 (S, 29)               | Ph 5 (S, 19)               | c12         | B         | 32.3                 | 34.9           | 48.3           | ns     |
| Ph 4 (S, 29)               | Ph 5 (NS, 52)              | c12         | B         | 42.4                 | 28.5           | 50.3           | ns     |
| e Ph 5 (S, 23)             | Ph 5 (NS, 108)             | g7          | C         | 12.2                 | 39.5           | 49.7           | ns     |
| e Ph 5 (S, 19)             | Ph 5 (NS, 52)              | c12         | C         | 30.6                 | 48.9           | 57.9           | ns     |
| e Ph 5 (NS, 108)           | 1 Ph 5 (NS, 77)            | g7          | D         | 47.4                 | 30.4           | 39.1           | < 0.05 |
| e Ph 5 (NS, 52)            | 1 Ph 5 (NS, 35)            | c12         | D         | 50.6                 | 46.8           | 59.1           | ns     |

Abbreviations: Ph, phase; e, early; l, late; S, silicified specimens from collections ICS-1173 and UCR 9963; NS, non-silicified specimens from collections ICS-1044 and UCR 9945; N, sample size; LM Config., landmark configuration; c8, 8 cephalic landmarks (see Fig. 24A); c12, 12 cephalic landmarks (see Figs 30A, 35A); g7, 7 glabellar landmarks (see Figs 23A, 34A); Ref. Form, reference form used in warp score calculation; A, consensus of smallest three specimens in phase 3; B, consensus of smallest three specimens in phase 4; C, consensus of smallest three silicified specimens in early phase 5; D, consensus of smallest six non-silicified specimens in early phase 5.
sagittal length approximately equal to that of anterior cephalic border. Maximum width of LA averages 111% basal glabellar width (tr.; Fig. 18C). Posterior margin of LO convex posteriorly. SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subquadrate to subtrapezoidal, slightly narrowing anteriorly, length (exsag.) averages 14% of glabellar length (sag.). S1 deepest abaxially, approximately parallel to SO or slightly more strongly anterolaterally orientated when traced abaxially. L1 subtrapezoidal, narrowing anteriorly; length (exsag.) averages 17% of glabellar length (sag.). S2 deepest in slot position, very shallowly connected to axial furrow (totally isolated from axial furrow on all but the smallest phase 5 cephalas), roughly transverse. L2 and L3 trapezoidal; merged distally on all but the smallest phase 5 cephalas, widening (tr.) anteriorly until contact with ocular lobes. S3 deepest in slot position, very shallowly connected to or essentially isolated from axial furrow, orientated anterolaterally away from axis until contact with ocular lobes. LA typically slightly wider (tr.) than long (sag.), approximately 40% of glabellar length (sag.), separated from extraocular area by a sharp break in slope, summit marginally higher than posterior glabellar segments and higher than summit of ocular lobes (Fig. 28A–G); widest point at contact with anterior margin of ocular lobes. Axial node on posterior margin of LO. Ocular lobes divergent from exsagittal axis by 6° to 9° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of inner margin of ocular lobe with abaxial margin of L3; Fig. 17F), crescentic, posterior tip transversely opposite midlength or anterior half of lateral margin of LO, flat-topped dorsally; extremely shallow ocular furrow sometimes present (Fig. 28A, E). Interocular area more or less horizontal or very gently sloping down adaxially in transverse section, approximately 85% to 100% as wide as ocular lobes (tr.) and approximately 50% to 64% width (tr.) of extraocular area opposite S1. Weak posterior ocular line or intergenal

Figure 27. Morphologically immature cephalas of *Olenellus gilberti* in phase 4 of development. A, UCR 9945.136, ×15; B, FMNH PE58452, ×15; C, CMC P2349d, ×15; D, FMNH PE58455, ×15. All internal moulds in dorsal view. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
Figure 28. Silicified morphologically immature cephalon of *Olenellus gilberti* in early phase 5 of development. A–D, dorsal, anterior, right lateral and posterior views, FMNH PE58457, ×10; E–G, dorsal, anterior and right lateral views, FMNH PE58458, ×10; H–J, dorsal, anterior and right lateral views, FMNH PE58459, ×10; K–N, dorsal, ventral, anterior and right lateral views, UCR 9963.147, ×10; O, P, dorsal and right lateral views, FMNH PE58460, ×10; Q–S, dorsal, anterior and right lateral views, FMNH PE58461, ×10. All from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
ridge sometimes present. Doublure runs around entire ventral margin, widest below lateral cephalic margins, narrowest below posterior cephalic border (narrowing adaxially) and posterior margin of LO (Fig. 28L).

**Subsequent change.** Intact silicified cephalae range in size up to almost 6 mm in sagittal length (Figs 3A, 29). Larger, intact silicified glabellae up to almost 7 mm long are also known, but these occur on otherwise fragmentary cephalae the original sagittal length of which cannot be reliably estimated. This size range is sufficient to permit analysis of ontogenetic shape change during the early portion of phase 5 of cephalic development, and meaningful comparison to that during phase 4, based purely on non-compact ed material.

Many aspects of growth remained allometric during early phase 5 of cephalic development. The glabella increased in proportional length relative to cephalic length (Fig. 18A) as LA proportionally elongated (sag.) and the preglabellar field proportionally shortened (sag.; Figs 28, 29). Glabellar lobe L2 proportionally widened (transversely), especially anteriorly, and the anterolateral portion of L2 merged with the posteralateral portion of L3, isolating S2 from the axial furrow, soon after entering phase 5 (Figs 28O, Q). The combined L2 + L3 structure proportionally shortened (exsag.). The ocular lobes progressively rotated into an orientation that is closer alignment to an exsagittal axis (Fig. 17F), and they progressively rotated into an orientation that is in closer alignment to the eye socle (Figs 28M–S, 29).

The rate of glabellar shape change relative to size significantly decreased upon entry into phase 5 (Fig. 23B; slope of reduced major axis for phase 4 \( n = 65 \) = 0.173; slope of reduced major axis for early phase 5 \( n = 23 \) = 0.081; slopes significantly different at 95% confidence).

Even amongst these non-compact ed specimens there is considerable variation in the position of the adgenal angle and the base of the intergenal spine relative to other landmarks, particularly during early phase 5. The additional variation around the average ontogenetic trajectory resulting from the inclusion of non-glabellar landmarks probably accounts for the fact that the pattern of overall cephalic shape change followed during phase 4 (Fig. 30F) is not determined to be statistically different from that followed during phase 5 (Fig. 30G; Table 3). The rate of cephalic shape change decreases upon entry into phase 5, but not significantly so (Fig. 30B; slope of reduced major axis for phase 4 \( n = 29 \) = 0.147; slope of reduced major axis for phase 5 \( n = 19 \) = 0.103; slopes not significantly different at 95% confidence).

The maximum size of intact, non-compact ed silicified specimens is considerably smaller than the maximum size of specimens preserved in a compacted state in shale (Fig. 3). Study of ontogenetic shape change over the entire size range of phase 5 cepha la therefore necessitates analysis of compacted specimens (Figs 6–14, 31–33), which introduces a significant taphonomic overprint on shape and shape variation (Webster & Hughes 1999; see below). Nevertheless, the quality of preservation of specimens from the Ruin Wash Lagerstätte is generally high despite the compaction, and the majority of cephalic shape variation amongst those specimens is attributable to ontogenetic shape change (compare Fig. 34D to Figs 34F, 34G; compare Fig. 35D to Fig. 35F, G). Relative to the shape difference between non-compact ed and compacted specimens (see below), shape difference between internal and external moulds of compacted specimens within shale is trivial (data not shown). Morphometric analyses of cephalae preserved in shale therefore used data extracted from well-preserved specimens irrespective of whether those specimens were internal or external moulds. (When internal and external moulds of the same specimen were available, data from only one mould were used.) Conclusions were not affected when analyses were repeated using data restricted to internal moulds alone or to external moulds alone (data not shown).

Geometric morphometric analyses of ontogenetic shape change during phase 5 based on specimens preserved in shale reveal that the glabella underwent a subtle but significant change in allometric patterning at a sagittal cephalic length of approximately 9.3 mm (compare
Figure 29. Silicified morphologically immature cephalas of *Olenellus gilberti* in early phase 5 of development. A–C, dorsal, anterior and left lateral views, FMNH PE58462, ×9; D–F, dorsal, anterior and right lateral views, FMNH PE58463, ×8; G–I, dorsal, right lateral and anterior views, FMNH PE58464, ×8; J–M, dorsal, ventral, anterior and left lateral views, UCR 9963.120, ×7. N, O, dorsal and right lateral views, FMNH PE58465, ×6; P–R, dorsal, right lateral and anterior views, FMNH PE58466, ×6; S, T, dorsal and left lateral views, UCR 9963.149, ×6; U, V, dorsal and left lateral views, FMNH PE58467, ×5. All from silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963).
Figure 30. Results of geometric morphometric analyses of patterns of ontogenetic shape change of morphologically immature cephalic of Olenellus gilberti. All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963; \( n = 54 \)). Symbols refer to phases of cephalic development: \( 	imes \), phase 4; \( \circ \), early phase 5; downward-pointing triangles indicate specimens of ambiguous phase assignment (i.e. either phase 4 or early phase 5). A, location of 12 cephalic landmarks used in the analyses. Paired homologous (non-sagittal) landmarks are shown only on the right side of the glabella for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, ‘rate’ of glabellar shape change as a function of cephalic size. Amount of shape change through ontogeny is quantified as Procrustes distance of each specimen away from the consensus configuration of the three smallest phase 4 specimens. Size is quantified as the natural logarithm of centroid size. Note slight decrease in ‘rate’ upon entry into early phase 5, as highlighted by LOWESS curve fitted to data. C, scatterplot of data on plane defined by first two principal components (PC1 and PC2) following PCA of warp scores (reference form = mean of all configurations). D, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 63.4% of total variance). Each higher PC accounts for less than 10% of total variance. E, thin-plate spline deformation grid showing shape variation when warp scores are regressed against the natural logarithm of centroid size (lnCS; reference form = consensus of three smallest phase 4 specimens). This linear regression model represents a crude approximation of ontogenetic shape change; note the similarity to D, F, G. F, thin-plate spline deformation grid showing pattern of ontogenetic shape change during phase 4 of cephalic development. Obtained by regressing warp scores against lnCS for phase 4 specimens only (\( n = 29 \); reference form = consensus of three smallest specimens in phase 4). G, thin-plate spline deformation grid showing pattern of ontogenetic shape change during early phase 5 of cephalic development. Obtained by regressing warp scores against lnCS for early phase 5 specimens only (\( n = 19 \); reference form = consensus of three smallest specimens in early phase 5). See text for details.
Fig. 34G–H, Table 3). Most notably, the proportional shortening (exsag.) of the L2 + L3 structure that was evident during early phase 5 (Figs 34G, 35G; also Figs 23I, 30G) effectively halted during late phase 5 (Figs 34H, 35H). Other ontogenetic trends of cephalic shape change in early phase 5, relating to proportional elongation and widening of LA, proportional shortening of the preglabellar field, rotation and proportional shortening of the ocular lobes, proportional widening of the extraocular area, and strengthening of the adgenal angle, persisted through late phase 5 of development (compare Fig. 35G to Fig. 35H). The position and strength of the adgenal angle and the position of the base of the intergenal spine are quite variable amongst cephalia in late phase 5 of development (see above; also Fig. 4A–C). This variation around the average ontogenetic trajectory probably accounts for the fact that the pattern of overall cephalic shape change followed during late phase 5 (Fig. 35H) is not determined to be statistically different from that followed during early phase 5 (Fig. 35G) when non-glabellar landmarks are included in the analysis (Table 3).

Non-silicified specimens in early phase 5 of cephalic development (Figs 31, 32, 33) provide ontogenetic information supplementing that available from silicified material (described above). Continuing a trend from phase 3, the posterior ocular line and intergenal ridge were progressively less prominent and/or expressed with decreasing frequency during later ontogeny, and both are often absent on cephalia in phase 5 of development. Similarly, an ocular furrow is often visible on cephalia in phase 4 of development.
development but is typically less prominent and/or expressed with lower frequency during phase 5. In contrast to the polarity of the above trends, some features were first expressed during early phase 5 of cephalic development and become more frequently visible on larger cephalon: extraocular genal caeca are first evident on non-silicified cephalon as small as approximately 3.4 mm in sagittal length; a genal ridge is first evident on non-silicified cephalon as small as 4.01 mm in sagittal length; and an anterior ocular line is first evident on non-silicified cephalon as small as 4.12 mm in sagittal length. Bertillon markings are first evident on the dorsal surface of LO of non-silicified cephalon as small as 3.95 mm in sagittal length, are first visible on L3 and LA of non-silicified cephalon as small as 6.03 mm in sagittal length, and first extend onto the ocular lobes of non-silicified cephalon as small as 6.34 mm in sagittal length. Terrace lines are first visible on the dorsal surface of the cephalic border of non-silicified cephalon as small as 5.37 mm in sagittal length.

Non-silicified specimens also provide information regarding the development of the trunk. A specimen approximately 3.45 mm in sagittal cephalic length and in late phase 4 or early phase 5 of cephalic development (Fig. 32A) preserves at least 11 prothoracic segments. The thorax of this specimen is elongate and triangular in outline; axial nodes are absent on T1 to T8 but present on T9 and T10 (the condition on T11 is unclear); T3 is strongly macropleural and the pleural furrow passes onto the base

Figure 32. Non-silicified morphologically immature specimens of Olenellus gilberti in early phase 5 of cephalic development showing details of cephalon and prothorax. A, latex cast of external mould, FMNH PE58470, ×7; B, internal surface of specimen preserved in calcite halo, UCR 9945.72, ×6; C, external surface of specimen preserved in calcite halo, UCR 9945.71, ×4; D, external mould, DMNH 16081, ×4; E, internal mould, FMNH PE58471, ×4; F, latex cast of external mould, FMNH PE58472, ×3. All from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945).
of the macrospinous pleural spine, the tips of which are not preserved; and the inner pleural regions are transversely orientated on T1 to T7 and become increasing divergent posterior to T8. Unfortunately, except for T3, thoracic pleural spines are not clearly preserved on this specimen.

A somewhat coarsely preserved specimen 3.64 mm in sagittal cephalic length and in early phase 5 of cephalic development (FMNH PE57515, not illustrated) shows a full complement of 14 prothoracic segments and a long axial spine on T15; any segments posterior to T15 are not preserved. Axial nodes are present on T10 to T14 of this specimen. Axial nodes on T1 and T2 were observed on specimens as small as 4.1 mm in sagittal cephalic length (FMNH PE57482, not illustrated). A better-preserved specimen 4.76 mm in sagittal cephalic length (Fig. 32B) also shows a full complement of 14 prothoracic segments and a long axial spine on T15; any segments posterior to T15 are again not preserved. Axial nodes are present on at least T8 to T14; T6 and T7 bear subtle axial swellings that might also represent incipient axial nodes.

The prothorax of specimens in early phase 5 of cephalic development (Figs 32, 33) is essentially identical to that of morphologically mature specimens (Figs 11–14, described above), except that the pleural spines of small specimens tend to be slightly thinner and more spindle-like: the
Figure 34. Results of geometric morphometric analyses of patterns of ontogenetic shape change of the glabella of *Olenellus gilberti* in phase 5 of cephalic development. All data from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945; internal and external moulds; \( n = 185 \)). Symbols refer to phases of cephalic development: open diamonds, early phase 5; crosses in boxes, late phase 5. A, location of seven landmarks around the periphery of the glabella used in the analyses. Paired homologous (non-sagittal) landmarks are shown only on the right side of the glabella for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, ‘rate’ of glabellar shape change as a function of glabellar size. Amount of shape change through ontogeny is quantified as Procrustes distance of each specimen away from the consensus configuration of the six smallest internal moulds in early phase 5. Size is quantified as the natural logarithm of centroid size. Regression line is a LOWESS curve fitted to data. C, scatterplot of data on plane defined by first two principal components (PC1 and PC2) following PCA of warp scores (reference form = mean of all configurations). D, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 42.11% of total variance). E, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 15.74% of total variance). Each higher PC accounts for less than 13% of total variance. F, thin-plate spline deformation grid showing shape variation when warp scores are regressed against the natural logarithm of centroid size (lnCS; reference form = consensus of six smallest internal moulds in early phase 5). This linear regression model represents a crude approximation of ontogenetic shape change; note the similarity to D, G. G, thin-plate spline deformation grid showing pattern of ontogenetic shape change during early phase 5 of cephalic development. Obtained by regressing warp scores against lnCS for early phase 5 specimens only (\( n = 108 \); reference form = consensus of six smallest internal moulds in early phase 5). H, thin-plate spline deformation grid showing pattern of ontogenetic shape change during late phase 5 of cephalic development. Obtained by regressing warp scores against lnCS for late phase 5 specimens only (\( n = 77 \); reference form = consensus of three smallest internal moulds in late phase 5). See text for details.
Figure 35. Results of geometric morphometric analyses of patterns of ontogenetic shape change of cephalic of *Olenellus gilberti* in phase 5 of development. All data from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945; internal and external moulds; \( n = 87 \)). Symbols refer to phases of cephalic development: open diamonds, early phase 5; crosses in boxes, late phase 5. A, location of 12 cephalic landmarks used in the analyses. Paired homologous (non-sagittal) landmarks are shown only on the right side of the glabella for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, ‘rate’ of cephalic shape change as a function of cephalic size. Amount of shape change through ontogeny is quantified as Procrustes distance of each specimen away from the consensus configuration of the three smallest cephala in early phase 5. Size is quantified as the natural logarithm of centroid size. Regression line is a LOWESS curve fitted to data. C, scatterplot of data on plane defined by first two principal components (PC1 and PC2) following PCA of warp scores (reference form = mean of all configurations). D, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 38.6% of total variance). E, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 21.48% of total variance). Each higher PC accounts for less than 11% of total variance. F, thin-plate spline deformation grid showing shape variation when warp scores are regressed against the natural logarithm of centroid size (InCS; reference form = consensus of three smallest cephala in early phase 5). This linear regression model represents a crude approximation of ontogenetic shape change; note the similarity to D, G. G, thin-plate spline deformation grid showing pattern of ontogenetic shape change during early phase 5 of cephalic development. Obtained by regressing warp scores against InCS for early phase 5 specimens only (\( n = 52 \); reference form = consensus of six smallest internal moulds in early phase 5). H, thin-plate spline deformation grid showing pattern of ontogenetic shape change during late phase 5 of cephalic development. Obtained by regressing warp scores against InCS for late phase 5 specimens only (\( n = 35 \); reference form = consensus of three smallest internal moulds in late phase 5). See text for details.
pleural spines became somewhat more robust and scythe-shaped during late phase 5, particularly at very large body size (Fig. 6C, D). Variation in the distribution of axial nodes on the prothorax of specimens in early phase 5 of cephalic development is statistically indistinguishable from that of specimens in late phase 5 of development (summarized above; discussed in more detail below). Bertillon markings on thoracic axial rings are evident on specimens at least as small as 7.85 mm in sagittal cephalic length (Fig. 32D). The mature morphology of *O. gilberti* (during late phase 5 of cephalic development) was described above.

**Development of the hypostome**

Silicified specimens reveal the ontogeny of the hypostome from a sagittal hypostomal length of approximately 0.61 mm (Fig. 19U) to approximately 7.5 mm (essentially morphologically mature; Fig. 36U–W). The mature morphology of the hypostome was described above (see also Fig. 10).

The smallest observed hypostome is associated with a fourth instar cephalon (Fig. 19U). The ventrally inflated portion of the anterior lobe of the middle body is subtriangular in outline (slightly wider anteriorly), almost twice as long (sag.) as wide (tr.), and occupies approximately three-fifths of the total sagittal length of the hypostome. Anterior to the anterior lobe is a broadly curved, narrow (sag.), crescentic structure that is more than four times as wide (tr.) between its distal tips as is the maximum width (tr.) of the ventrally inflated portion of the anterior lobe of the middle body. Given the rather coarse preservation of the specimen it is unclear whether this structure represents the rostral plate, a transversely elongate extension of the anterior margin of the hypostome, or a combination of the two. The anterior wings of the hypostome must lie somewhere along, or at the distal tips of, this crescentic structure. The posterior lobe of the middle body forms a broad crescentic band that wraps around the posterior half of the anterior lobe. The maximum width (tr.) of the hypostome across the posterior lobe is approximately 80% of the maximum hypostome length. The posterior margin bears tiny projections giving it a serrated appearance, but the number of these projections is unclear due to the coarse preservation. The hypostome occupies approximately 60% of the ventral cephalic length (sag.), with the posterior margin of the hypostome apparently lying a little more than one-fifth of the posterior-to-anterior distance along the sagittal axis of the cephalon. The nature of any connection between the anterior margin of the hypostome and the narrow, crescentic rostral plate is unclear: the two may be fused or, perhaps more likely given the apparent dissociation of the sclerites on some specimens (Fig. 19V), either abut along a hypostomal suture (of unknown length) or even not be in direct contact.

During subsequent development, the anterior lobe of the middle body progressively proportionally expanded (tr. and sag.) and became more ventrally convex in cross section (tr. and sag.), so that it changes in ventral outline...
from subtriangular (Fig. 36A) to egg-shaped (Fig. 36E) to suboval (Fig. 36I, M) to subcircular (Fig. 36Q, U). The anterior margin developed a well-defined, narrow (exsag.) border that bears a median notch formed by an anterovelar deflection of the border on the sagittal axis (Fig. 36C, G, K, O, S). The anterior border proportionally narrowed (exsag.) over ontogeny and is wire-like (especially exsagittally) on hypostomes larger than 3.4 mm (sag.: Fig. 36Q, R). The anterior wings progressively migrated posteriorly during hypostome ontogeny, the tips being located transversely opposite a point approximately 30% to 40% of the anterior-to-posterior distance along the sagittal axis of the hypostome on hypostomes smaller than 1.8 mm in sagittal length (Fig. 36B, F, J, N), 40% to 50% of the anterior-to-posterior distance along the sagittal axis of the hypostome on larger hypostomes (Fig. 36R), and probably slightly posterior to the hypostomal midlength on the largest silicified specimen (Fig. 36V).

The posterior lobe of the middle body proportionally shortened (sag.) and narrowed (tr.) as the anterior lobe proportionally enlarged; the maximum width (tr.) across the posterior lobe is exceeded by the maximum width (tr.) across the anterior lobe of the middle body (excluding the anterior wings) on hypostomes larger than 1.7 mm in sagittal length (Fig. 36Q, U). The posterior margin of the posterior lobe is evenly curved on hypostomes smaller than 1.0 mm in sagittal length (Fig. 36A, E), but became straighter across the sagittal axis during subsequent ontogeny (Fig. 36I, M, Q, U). The maculae are shallower on the smallest hypostomes (Figs 19U, 36A) but proportionally deepened and became less steeply posteriorly orientated (when traced adaxially), especially adaxially, during subsequent ontogeny (Fig. 36E, I, M, Q, U). Ovate swellings adjacent to the posterolateral corners of posterior lobe are evident on hypostomes larger than 3.4 mm in sagittal length (Fig. 36Q, U).

Six pairs of spines are present along the lateral and posterolateral margin of the posterior lobe of hypostomes 0.9 mm to 1.2 mm in sagittal length (Fig. 36A, E); no spine seems to be developed on the sagittalmost portion of the posterior margin. The anteriormost (outermost) pair of spines project laterally with only a weak posterior component to their orientation; more posterior spines are oriented progressively more strongly posteriorly, and the posteriormost (innermost) pair of spines project directly posteriorly or are weakly convergent posteriorly. Each spine pair has a unique shape, ranging from fairly straight (outermost pair) to strongly geniculated, to gently curved (innermost pairs). The distal portion of each spine is open dorsally and presumably not mineralized in life (Fig. 36G). The spines are slightly less than half as long as the sagittal length of the posterior lobe of the middle body on these small specimens (Fig. 36A, E). During subsequent ontogeny, the distance between the innermost pair of spines proportionally increased so that all the spines became progressively restricted to the lateral border, and all the spines became progressively proportionally smaller (Fig. 36E, I). On hypostomes larger than 3.4 mm in sagittal length the spines are represented only as tiny spinelets or nubbins, giving the lateral border a serrated appearance (Fig. 36Q, U).

The hypostomal doublure is developed only around the margins of the posterior lobe of the middle body, and is initially of relatively uniform width (Fig. 36D, H). During subsequent ontogeny the entire doublure, and particularly the medial portion, proportionally narrowed to a thin lip (Fig. 36L, P, T, W). An ornament of concentric Bertillon markings on the anterior lobe of the middle body is visible on the ventral surface of hypostomes at least as small as approximately 7.5 mm in sagittal length (Fig. 36U, V).

**Intraspecific variation**

As highlighted in the Introduction, consideration of the structure and magnitude of intraspecific variation can have great bearing on our understanding of evolutionary patterns and processes, and is critical to species diagnosis and related issues such as diversity estimation and biostatigraphical correlation. In the sections that follow, the magnitude and nature of intraspecific variation within *Olenellus gilberti* is therefore investigated in considerable detail. These data will serve as an empirical baseline for character analysis in future studies of olenelloid palaeobiology and evolution. First, the effect of taphonomic compaction on cephalic shape is explored. This identifies the magnitude and structure of taphonomic overprint on fossil form, and thus offers insight into the limits of palaeobiological questions that might be addressable when only compacted material is available. Second, variation in cephalic size and shape over ontogeny are explored. This permits determination of whether these traits were poorly constrained during development, as might be predicted if developmental processes were only weakly canalized in early trilobites (as proposed by, for example, McNamara 1986). Third, the structure of non-ontogenetic cephalic shape variation is quantitatively explored for phase 4, early phase 5 and late phase 5 of development. Comparison of such static variation to the pattern of dynamic (ontogenetic) variation within each phase allows assessment of whether static variation was potentially governed by the same factors that governed ontogenetic shape change, and thus whether intraspecific heterochrony was an important contributor to size-independent shape variation. Finally, variation in qualitative and meristic traits of the mature cephalon, prothorax and opisthothorax are assessed. Intraspecific variation in such qualitative and meristic traits is more readily compared amongst disparate trilobite species than is intraspecific variation in shape, and
these data can be used to determine whether the degree of variation within *O. gilberti* was higher than that of later and more derived trilobites (see Discussion, below).

### Effects of taphonomic compaction on cephalic shape

The effects of taphonomic compaction on the morphology of *Olenellus gilberti* were previously investigated by Webster & Hughes (1999). That study compared cephalic shape and shape variation between non-compacted (silicified) and compacted (in shale) specimens from the same collections as studied here. Specimens of a comparable size range were studied for each sample. The effects of compaction were then visualized as the difference in mean shape between samples, and quantified as the change in variation around the average ontogenetic trajectory for each cephalic landmark over the sampled portion of ontogeny between samples. The earlier study is expanded upon here, exploiting a larger sample size of silicified and non-silicified specimens and more refined morphometric techniques. These techniques allow (1) explicit comparison of ontogenetic trajectories between samples using the entire landmark configuration rather than on a landmark-by-landmark basis; and (2) size-standardization of shape, permitting between-sample comparisons of mean cephalic shape and variance with the effects of ontogenetic allometry analytically removed. As for the earlier study, this assumes that any observed differences between samples (controlling for ontogeny) are attributable to taphonomy rather than to the small geographical and stratigraphical separation of the collections.

Whether using a landmark configuration summarizing the shape of the glabella or of the entire cephalon, the ontogenetic trajectory of shape change during early phase 5 based on data from silicified specimens is statistically indistinguishable from that based on data from non-silicified specimens (Table 3). The significant shift in allometric patterning of the glabella upon entry into early phase 5 detected using silicified specimens is also detected using data from non-silicified specimens (Table 3). Morphometric data for the entire cephalon fail to detect a significant change in allometric patterning upon entry into early phase 5 whether those data were extracted from silicified or non-silicified specimens (Table 3).

Within each of the silicified and non-silicified samples, the pattern of ontogenetic shape change was constant during early phase 5, as revealed by a linear relationship between shape variables (warp scores) and specimen size (lnCS) (data not shown). Size-standardization of the shape data based on linear regression is therefore appropriate. Cephalic landmark configurations of both samples were size-standardized to lnCS = 2.1, corresponding to a cephalic length of approximately 5.6 mm. This is within the size range of both samples, and so the size-standardization procedure did not involve extrapolation of the linear regression beyond observed values. At this size, the mean shape of silicified specimens significantly differs from the mean shape of non-silicified specimens (Table 4; Fig. 37). On non-silicified specimens the glabella is typically proportionally longer (particularly along LA) and wider (tr., particularly across LO and LA), the posterior tip of the ocular lobe is typically located slightly closer to the glabella, and the genal region (including the adgenal angle and the base of the genal spine) is typically more anterolaterally located (Fig. 37; compare also cephalon in Figs 28, 29 to those in Figs 31, 32, 33). These morphological differences suggest that compaction caused a collapse of LA, a slight lateral splaying of the glabella, and a pronounced lateral splaying of the abaxial portion of the cephalon. Such a pattern is consistent with fracture patterns on compacted cephalon (Webster & Hughes 1999).

Size-standardized shape variance within early phase 5 is significantly higher within the non-silicified sample than within the silicified sample (Table 5, Fig. 38). For landmark configurations summarizing the shape of either just the glabella or the glabella plus the rest of the cephalon, shape variance in the non-silicified sample is more than double that of the silicified sample. It is conceivable that some of this higher variance might be attributable to the absence from the silicified sample of large cephalon in early phase 5 of development. Such larger specimens might have exhibited greater residuals from the estimation of mean form following size-standardization and thus increased shape variance. However, shape variance does not increase through phase 5 of cephalic development.

| Sample 1 (preservation, N) | Sample 2 (preservation, N) | LM Config. | Distance between means | 95% Confidence limits | F-score | P-value |
|----------------------------|----------------------------|------------|------------------------|-----------------------|---------|---------|
| Sil (23)                   | Non-sil (108)              | g7         | 0.025                  | 0.0209–0.0307         | 8       | 0.0006  |
| Sil (19)                   | Non-sil (52)               | c12        | 0.0288                 | 0.0231–0.0381         | 6.11    | 0.0006  |

Abbreviations: Sil, silicified specimens from collections ICS-1173 and UCR 9963; Non-sil, non-silicified specimens from collections ICS-1044 and UCR 9945; N, sample size; LM Config., landmark configuration; g7, 7 glabellar landmarks (see Figs 23A, 34A); c12, 12 cephalic landmarks (see Fig. 37A).
taphonomic compaction, as described in the text. In mean shape between these samples is attributable to effects of inter-sample difference in average size has been analytically removed by size-standardization, and observed difference due to ontogenetic allometry having been analytically removed. Compaction did not significantly alter the average size-clusters using these variables (above; Fig. 16B, D). The effect of compaction on fossil form.

The variance of a log-transformed size variable $X$ from one instar ($i$) to the next ($i + 1$) can lead to insight regarding the regulation of growth. This is because

$$\text{var}(X_{i+1}) = \text{var}(X_i) + \text{var}(D) + 2\text{cov}(X_i, D),$$

where $D$ is the log-transformed value of Dyar’s coefficient (e.g. Klingenberg 1996, p. 2424; Fusco et al. 2004, pp. 171–172). The variance of $D$ can be directly measured in longitudinal studies of ontogeny (i.e. with repeated measurement of individuals through their respective ontogenies) and is always larger than zero due to the influence of external factors such as temperature and nutritional condition (e.g. Klingenberg 1996). In such longitudinal studies, a constant or decreasing variance in log-transformed traits through successive instars is therefore evidence of a negative covariance between the log-transformed trait and $D$. A negative covariance between size of a trait in one instar and growth ratio to the next instar is indicative of tight regulation of growth, whereby individuals that are larger than average at one instar undergo less growth into the next instar relative to smaller individuals, and vice versa. This phenomenon is variously termed regulative growth, compensatory growth, convergent growth, or targeted growth (e.g. Riska et al. 1984 and references therein; Klingenberg 1996; Fusco et al. 2004).

Cephalic size and shape variation during ontogeny

Variation in cephalic size over instars 1 to 5. The dearth of clearly defined landmarks prohibits meaningful geometric morphometric analysis of cephalic shape on instars 1 to 5 (Figs 19, 20). Instead, variation within each of these instars is explored and quantified through two size measures: sagittal cephalic length and the transverse distance between the bases of the intergenal spines (intergenal spine separation). The instars can be discerned as size-clusters using these variables (above; Fig. 16B, D).

Change in the variance of a log-transformed size variable $X$ from one instar ($i$) to the next ($i + 1$) can lead to insight regarding the regulation of growth. This is because

$$\text{var}(X_{i+1}) = \text{var}(X_i) + \text{var}(D) + 2\text{cov}(X_i, D),$$

where $D$ is the log-transformed value of Dyar’s coefficient (e.g. Klingenberg 1996, p. 2424; Fusco et al. 2004, pp. 171–172). The variance of $D$ can be directly measured in longitudinal studies of ontogeny (i.e. with repeated measurement of individuals through their respective ontogenies) and is always larger than zero due to the influence of external factors such as temperature and nutritional condition (e.g. Klingenberg 1996). In such longitudinal studies, a constant or decreasing variance in log-transformed traits through successive instars is therefore evidence of a negative covariance between the log-transformed trait and $D$. A negative covariance between size of a trait in one instar and growth ratio to the next instar is indicative of tight regulation of growth, whereby individuals that are larger than average at one instar undergo less growth into the next instar relative to smaller individuals, and vice versa. This phenomenon is variously termed regulative growth, compensatory growth, convergent growth, or targeted growth (e.g. Riska et al. 1984 and references therein; Klingenberg 1996; Fusco et al. 2004).

Figure 37. Effects on compaction on size-standardized shape of cephalia in early phase 5 of development. A, location of 12 cephalic landmarks used in the analysis. Paired homologous (non-sagittal) landmarks are shown only on the right side of the cephalon for clarity, but their coordinates were digitized on both sides and then computationally reflected across the midline (left onto right) and averaged to reduce data redundancy, as described in the text. B, thin-plate spline deformation grid showing shape change from mean shape of size-standardized silicified cephalia (from silicified bed at Hidden Valley; collections ICS-1173 and UCR 9963; n = 19) to mean shape of size-standardized non-silicified cephalia (from Ruin Wash Lagerstätte; collections ICS-1044 and UCR 9945; n = 52). Shape difference between samples due to inter-sample difference in average size has been analytically removed by size-standardization, and observed difference in mean shape between these samples is attributable to effects of taphonomic compaction, as described in the text.

(see below), and it is likely that the vast majority of the difference in variance between the samples results from the effect of compaction on fossil form.

In this particular case, taphonomic compaction therefore caused a significant change in mean fossil form and an increase in shape variance (with shape variance attributable to ontogenetic allometry having been analytically removed). Compaction did not significantly alter the average ontogenetic trajectory of cephalic shape change, but did inflate the variance in shape around that trajectory. The effect of compaction can therefore be envisioned as to cause a step-like shift of the location of an ontogenetic trajectory of shape change within a morphospace, and an increase in variance around that trajectory, but not a change in the orientation of that trajectory through the morphospace. These results complement and are consistent with those of an earlier study (Webster & Hughes 1999). These findings demonstrate that many aspects of biological (pre-compactional) shape and shape variation (including ontogenetic shape change) are distorted and blurred by taphonomic compaction of fossils. Whether the magnitude of this compaction-related shape distortion is problematic to any investigation will depend on the nature of that investigation. The effects of compaction-related deformation of a sample may be a serious hindrance when that sample is being compared to a (non-compacted) sample of close morphological similarity, but may be negligible in broader studies of disparity. This will be further investigated in a study of disparity amongst olenelloid trilobites (to be published elsewhere).
The variance of log-transformed cephalic length does not significantly change through instars 1 to 5 of *Olenellus gilberti* (Fig. 16E). Over the same portion of ontogeny the variance of log-transformed intergenal spine separation shows a significant decline (Fig. 16F). Under the reasonable assumption that the variance of \( D \) was larger than zero in trilobites just as it is in extant arthropods (see Fusco et al. 2004), these data are consistent with *O. gilberti* having exhibited targeted growth in these traits through the early portion of its ontogeny. This would represent the oldest known case of targeted growth within metazoans (the record previously being held by the Silurian trilobite *Aulacopleura konincki* (Barrande, 1846); Fusco et al. 2004; but see below). However, studies of trilobite ontogeny invariably rely on cross-sectional data, where each individual is measured just once and data from successive instars are taken from different sets of individuals, and this creates ambiguity in the interpretation of these data. In studies based on cross-sectional data it is conceivable that a constant or decreasing variance in log-transformed traits through successive instars could result from constant or increasing selection against deviant phenotypes, irrespective of the sign and magnitude of the covariance between \( X_i \) and \( D \). (Although not realized

| Sample | Pres. | LM Config. | N | lnCS | Variance | 95% Confidence limits | Variance | 95% Confidence limits |
|--------|-------|------------|---|------|----------|-----------------------|----------|-----------------------|
| Ph 3   | S     | g8         | 18 | 0.33 | 0.00097  | 0.00071–0.00114       | 0.00109  | 0.00083–0.00125       |
| Ph 3   | S     | g7         | 20 | 0.33 | 0.00080  | 0.00057–0.00098       | 0.00096  | 0.00074–0.00111       |
| Ph 4   | S     | g8         | 59 | 0.66 | 0.00091  | 0.00075–0.00103       | 0.00138  | 0.00114–0.00156       |
| Ph 4   | S     | g7         | 65 | 0.67 | 0.00079  | 0.00067–0.00089       | 0.00125  | 0.00104–0.00144       |
| Ph 4   | S     | c12        | 29 | 1.36 | 0.00099  | 0.00080–0.00112       | 0.00155  | 0.00113–0.00192       |
| e Ph 5 | S     | g7         | 23 | 1.6  | 0.00068  | 0.00052–0.00077       | 0.00092  | 0.00071–0.00106       |
| e Ph 5 | S     | c12        | 19 | 2.1  | 0.00088  | 0.00066–0.00104       | 0.00112  | 0.00076–0.00151       |
| e Ph 5 | NS    | g7         | 108| 1.6  | 0.00165  | 0.00140–0.00185       | 0.00189  | 0.00160–0.00212       |
| e Ph 5 | NS    | c12        | 52 | 2.1  | 0.00225  | 0.00186–0.00256       | 0.00257  | 0.00214–0.00293       |
| l Ph 5 | NS    | g7         | 77 | 2.35 | 0.00175  | 0.00147–0.00202       | 0.00192  | 0.00161–0.00218       |
| l Ph 5 | NS    | c12        | 35 | 2.9  | 0.00229  | 0.00184–0.00273       | 0.00249  | 0.00192–0.00297       |

Abbreviations: Ph, phase; e, early; l, late; Pres., preservation; S, silicified specimens from collections ICS-1173 and UCR 9963; NS, non-silicified specimens from collections ICS-1044 and UCR 9945; LM Config., landmark configuration; c12, 12 cephalic landmarks (see Figs 30A, 35A); g7, 7 glabellar landmarks (see Figs 23A, 34A); g8, 8 glabellar landmarks (see Fig. 22A); N; sample size; lnCS, natural logarithm of centroid size to which configurations were size-standardized.

The variance of log-transformed cephalic length does not significantly change through instars 1 to 5 of *Olenellus gilberti* (Fig. 16E). Over the same portion of ontogeny the variance of log-transformed intergenal spine separation shows a significant decline (Fig. 16F). Under the reasonable assumption that the variance of \( D \) was larger than zero in trilobites just as it is in extant arthropods (see Fusco et al. 2004), these data are consistent with *O. gilberti* having exhibited targeted growth in these traits through the early portion of its ontogeny. This would represent the oldest known case of targeted growth within metazoans (the record previously being held by the Silurian trilobite *Aulacopleura konincki* (Barrande, 1846); Fusco et al. 2004; but see below). However, studies of trilobite ontogeny invariably rely on cross-sectional data, where each individual is measured just once and data from successive instars are taken from different sets of individuals, and this creates ambiguity in the interpretation of these data. In studies based on cross-sectional data it is conceivable that a constant or decreasing variance in log-transformed traits through successive instars could result from constant or increasing selection against deviant phenotypes, irrespective of the sign and magnitude of the covariance between \( X_i \) and \( D \). (Although not realized

Figure 38. Variance in size-standardized shape of *Olenellus gilberti* through phase 3, phase 4, early phase 5 and late phase 5 of development. Circles indicate shape variance for non-compacted, silicified cepha (from silicified bed at Hidden Valley; collections ICS-1173 and UCR 9963). Triangles indicate shape variance for compacted cephalia preserved in shale (from Ruin Wash Lagerstätte; collections ICS-1044 and UCR 9945; data from internal and external moulds). Error bars indicate upper and lower 95% confidence limits around variance, based on bootstrap resampling (1600 replicates). A, variance in shape of the glabella, as summarized by seven landmarks around the periphery of that structure (landmark locations shown on specimen in upper left corner); B, variance in cephalic shape, as summarized by 12 landmarks (landmark locations shown on specimen in upper left corner). For both landmark configurations, compaction significantly increases shape variance but, when preservational state is held constant, variance does not significantly change (at 95% confidence) over the sampled portion of ontogeny. See text for interpretation.
by those authors, this ambiguity in interpretation also applies to the earlier study of growth regulation in *A. konincki* by Fusco et al. [2004]).

Distinguishing a hypothesis of constant or increasing selection against deviant phenotypes from one of targeted growth requires either longitudinal data or knowledge regarding the selectivity of deaths, and is thus impossible for trilobites. The data presented herein (Fig. 16E, F) therefore demonstrate either (1) the oldest known case of targeted growth in animal history; or (2) the existence of strong (and increasing) selective pressure on two size variables during the early ontogenetic stages of an early Cambrian trilobite. The evolutionary implications of these interpretations are discussed below.

**Variation in cephalic shape over later portions of ontogeny.** Comparison of shape variation amongst different stages of ontogeny is most meaningful when within-stage variation due to ontogenetic allometry is controlled. Ideally, this would involve instar-to-instar comparison. However, the paucity of landmarks on small cephalas mean that geometric morphometric analysis of shape variation in *Olenellus gilberti* can only be performed on cephalas in late phase 3 of development and beyond. Data from such relatively large specimens do not form discrete size-clusters, and instars cannot be recognized (see section on instar recognition, above). Instead, specimens are herein pooled by phase of cephalic development. The ontogenetic trajectory of shape change within any phase is linear (data not shown), so that size-standardization of shape data within that phase is appropriate (see Material and methods, above). Data for each phase were size-standardized to the median lnCS value for that particular phase. The remaining shape variation therefore represents an estimate of ‘static’ variation around the average shape for cephalas within that phase of development, with the effects of allometry having been analytically removed. This permits a phase-to-phase comparison of shape variation through ontogeny.

As expected, size-standardization consistently results in a decrease in shape variation within each phase relative to the non-size-standardized data (Table 5). The decrease is significant (at 95% confidence) for phase 4 for each of the three landmark configurations analysed. This is also the phase associated with the most dramatic ontogenetic shape change amenable to geometric morphometric analysis. Size-related shape variation was therefore a major component of shape variation within each phase. This is consistent with the close similarity between the shape variation described by the first principal component and the general pattern of ontogenetic shape change over the sampled portion of ontogeny (compare Fig. 22D to Fig. 22F, Fig. 23D to Fig. 23F, and Fig. 30D to Fig. 30E).

Whether based on glabellar or on overall cephalic shape, ‘static’ shape variance does not significantly change (at 95% confidence) from phase 3 to phase 4, from phase 4 to early phase 5 (based on silicified specimens), or from early to late phase 5 (based on non-silicified specimens) (Table 5; Fig. 38). (The significantly higher variance of non-silicified samples relative to silicified samples is discussed in the section on taphonomic compaction, above). This essentially constant variance is counter to the common expectation of increasing variation through ontogeny (built on the reasonable assumption that variation should be continually generated through development), and suggests that either (1) shape variation was developmentally regulated, or (2) there was selection against deviant phenotypes. The evolutionary implications of these observations are discussed below.

**Structure of cephalic shape variation**

The structure of cephalic shape variation was explored separately for phase 4, early phase 5 and late phase 5 by conducting a PCA of the size-standardized shape data (partial warp scores including the two uniform terms, using the consensus of all configurations in that sample as the reference form) for each (portion of) a phase in turn. Analysis of the size-standardized data (with size-related shape change analytically removed) results in a summary of the structure of size-independent (i.e. ontogenetically static) shape variation within each phase. This technique has been previously applied to ptychoparioid trilobites (Webster 2011a).

For silicified cephalas in phase 4 of development, 64% of the total size-standardized shape variation is summarized by the first three PCs (Fig. 39). PC1 accounts for 26% of the total size-standardized shape variation, and relates primarily to variation in the length of the posterior cephalic margin between the axial furrow and the adgenal angle, in the length of LA relative to the length of L2 + L3, in the proximity of the posterior tip of the ocular lobe to the axial furrow, and in the separation of the adgenal angle from the base of the genal spine (Fig. 39C). PC2 accounts for 21% of the total size-standardized shape variation, and relates primarily to variation in the strength and anteroposterior location of the adgenal angle (Fig. 39D). PC3 accounts for 17% of the total size-standardized shape variance, and relates primarily to local variation in the exsagittal length of the ocular lobes and posterior portion of LA (Fig. 39E). Higher PCs each account for less than 9% of the total size-standardized shape variation and are not considered herein.

For silicified cephalas in early phase 5 of development, 65% of the total size-standardized shape variation is summarized by the first three PCs (Fig. 40). PC1 accounts for 30% of the total size-standardized shape variation, and relates primarily to variation in the length of LA relative to the rest of the glabella and to the preglabellar field, in the width of L2 + L3 relative to more posterior glabellar
lobes, in the relative length of the ocular lobe, in the transverse width of the posterior portion of the extraocular area, and in the angle and degree of separation of the base of the genal spine from the adgenal angle (Fig. 40C). PC2 accounts for 22% of the total size-standardized shape variation, and relates primarily to variation in the size of the preglabellar field relative to the length of LA (Fig. 40D). PC3 accounts for 13% of the total size-standardized shape variation, and relates primarily to variation in the location of the adgenal angle along the posterior cephalic margin (Fig. 40E). Higher PCs each account for less than 9% of the total size-standardized shape variation and are not considered herein.

For non-silicified cephalia in early phase 5 of development, 74% of the total size-standardized shape variation is summarized by the first three PCs (Fig. 41). PC1 accounts for 38% of the total size-standardized shape variation, and relates primarily to variation in the size of the glabella relative to the preglabellar field, in the transverse width of LA and L2 + L3 relative to more posterior glabellar lobes, in the proximity of the posterior tip of the ocular lobe to the glabella, in the transverse width of the posterior portion of the extraocular area, and in the angle and degree of separation of the base of the genal spine from the adgenal angle (Fig. 41C). PC2 accounts for 23% of the total size-standardized shape variation, and relates primarily to variation in the length of the glabella (especially LA) relative to cephalic width, in the proximity of the posterior tip of the ocular lobe to the glabella, and in the anteroposterior location of the adgenal angle and base of the genal spine relative to the glabella (Fig. 41D). PC3 accounts for 13% of the total size-standardized shape variation, and relates primarily to variation in the location of the adgenal angle along the posterior cephalic margin (Fig. 41E). Higher PCs each account for less than 7% of the total size-standardized shape variation and are not considered herein.

Many aspects of these major components of shape variation are also detected in the analysis of silicified cephalia in early phase 5 of development (above; Fig. 40). The
differences in the structure of shape variation are attributable to taphonomic compaction and/or the more limited size range of silicified cephalas in early phase 5 of development (see above).

For non-silicified cephalas in late phase 5 of development, 63% of the total size-standardized shape variation is summarized by the first two PCs (Fig. 42). PC1 accounts for 43% of the total size-standardized shape variation, and relates primarily to variation in the relative length of the ocular lobe, in the length of the preglabellar field relative to the glabella and anterior cephalic border, and in the strength of the adgenal angle (Fig. 42B). PC2 accounts for 20% of the total size-standardized shape variation, and relates primarily to localized variation in the anteroposterior location of the genal spine base relative to the adgenal angle (Fig. 42C). It is driven by a single specimen with strongly advanced genal spine bases which are located transversely opposite SO (Fig. 42A; ICS-1044.76a, not illustrated). Higher PCs each account for less than 10% of the total size-standardized shape variation and are not considered herein.

It is intriguing that within each portion of ontogeny studied here, the dominant structure of size-standardized shape variation is generally similar to the pattern of cephalic shape change during that portion of ontogeny: for phase 4 compare Fig. 39C to Fig. 30F (the polarity of PC1 is arbitrary and in this case is reversed relative to the direction of ontogenetic shape change); for early phase 5 compare Fig. 40C to Fig. 30G or Fig. 41C to Fig. 35G; for late phase 5 compare Fig. 42B to Fig. 35H. This suggests that anatomical regions that covary in shape during ontogeny might also co-vary in shape when static (non-ontogenetic) variation alone is considered. The evolutionary implication of this potential parallelism between the structure of ontogenetic shape variation and the dominant structure of static shape variation is discussed below.

Variation in qualitative and meristic characters at maturity

In order to maximize potential phylogenetic signal, recent studies of olenelloid systematics and evolution have

![Figure 40. Results of PCA of warp scores exploring structure of size-standardized shape variation amongst silicified cephalas of Olenellus gilberti in early phase 5 of development. All data from specimens in silicified bed at Hidden Valley (collections ICS-1173 and UCR 9963; n = 19). Based on analysis of 12 cephalic landmarks as shown in Figs 30A, 35A; reference form = mean of all specimens. A, scatterplot of data on plane defined by first two principal components (PC1 and PC2); B, scatterplot of data on plane defined by PC1 and PC3; C, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 30% of total variance); D, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 22% of total variance); E, thin-plate spline deformation grid showing shape variation along PC3 in a positive direction (accounting for 13% of total variance). See text for details.](image-url)
Figure 41. Results of PCA of warp scores exploring structure of size-standardized shape variation amongst non-silicified cephalas of *Olenellus gilberti* in early phase 5 of development. All data from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945; internal and external moulds; *n* = 52). Based on analysis of 12 cephalic landmarks as shown in Figs 30A, 35A; reference form = mean of all specimens. **A**, scatterplot of data on plane defined by first two principal components (PC1 and PC2); **B**, scatterplot of data on plane defined by PC1 and PC3; **C**, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 38% of total variance); **D**, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 23% of total variance); **E**, thin-plate spline deformation grid showing shape variation along PC3 in a positive direction (accounting for 13% of total variance). See text for details.

Figure 42. Results of PCA of warp scores exploring structure of size-standardized shape variation amongst non-silicified cephalas of *Olenellus gilberti* in late phase 5 of development. All data from Ruin Wash Lagerstätte (collections ICS-1044 and UCR 9945; internal and external moulds; *n* = 35). Based on analysis of 12 cephalic landmarks as shown in Figs 30A, 35A; reference form = mean of all specimens. **A**, scatterplot of data on plane defined by first two principal components (PC1 and PC2); **B**, thin-plate spline deformation grid showing shape variation along PC1 in a positive direction (accounting for 43% of total variance); **C**, thin-plate spline deformation grid showing shape variation along PC2 in a positive direction (accounting for 20% of total variance). See text for details.
considered a wide range of aspects of morphology from all parts of the dorsal exoskeleton (e.g. Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Lieberman 1998, 1999). Some of these relate to the shape or to the relative size of structures, and are therefore best treated as continuously varying traits (at least during data collection, even if those trait values are ultimately binned into discrete states for cladistic analysis). Others relate to features that are best described in qualitative (e.g. presence/absence) or meristic (integer count) terms. Variation in shape and in continuously varying quantitative characters amongst morphologically mature and immature specimens of *Olenellus gilberti* are documented above. Variation in qualitative and meristic aspects of mature morphology is explored in this section. The evolutionary significance of this variation is discussed below.

**Cephalon.** The presence or absence (and sometimes prominence) of extraocular genal caeca, an anterior ocular line, a genal ridge, an intergenal ridge, and an ocular furrow have all been considered to be relevant to olenelloid systematics and phylogeny (e.g. Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Lieberman 1998, 1999). The presence or absence of a posterior ocular line has not been used as a character in cladistic analyses, but is another prominent ridge-like feature on the cephalon that deserves consideration in character analysis. Intraspecific variation in the presence or absence of each of these features has been documented in recent studies of other olenelloid species (Webster 2007b, c, 2009a), but those studies did not quantify the frequency of development of the features within those species. The frequency of presence of these features in morphologically mature specimens (i.e. cephalon in late phase 5 of development) of *Olenellus gilberti* is quantified here. The percentages quoted below represent the proportion of sufficiently well-preserved individuals (represented by internal and/or external moulds) upon which the particular feature was visible. Specimens for which the failure to observe a particular feature might be a result of preservation (e.g. the extraocular area was poorly preserved or partially obscured) were omitted from the tally. Ranges in parentheses following each percentage represent two-unit profile likelihood confidence intervals.

Extraocular genal caeca are present on 77% (70–83%) of morphologically mature cephalon of *O. gilberti*. An anterior ocular line is very rarely developed, being present on just 1% (0–4%) of morphologically mature cephalon studied herein. Similarly, an intergenal ridge is present on just 2% (0–4%) of specimens. A genal ridge is more frequently expressed, being visible on 36% (29–44%) of specimens, and a posterior ocular line is present on 10% (6–16%) of specimens. An ocular furrow is visible on 29% (23–37%) of specimens.

As has been documented for other olenelloids (e.g. Webster 2009a), the presence or absence and degree of expression of each of these features can vary not only amongst conspecific specimens but also on the external versus interval surface of a single cephalon. Not surprisingly, extraocular genal caeca, the various ridges and lines, and ocular furrows are typically more prominently developed on internal moulds (i.e. the side of the exoskeleton in contact with the animal’s tissue). Indeed, a genal ridge is visible with significantly greater frequency on internal moulds than on external moulds (present on 52% [41–63%] of specimens represented solely as internal moulds and on just 15% [8–27%] of specimens represented solely as external moulds). However, the proportion of specimens bearing extraocular genal caeca, an anterior ocular line, a posterior ocular line, an intergenal ridge, and an ocular furrow did not significantly differ between internal and external moulds (data not shown).

**Prothorax.** The presence or absence of axial nodes on prothoracic segments has been deemed to be phylogenetically informative regarding relationships within the Olenelloidea (Lieberman 1998 [character 66]). The distribution of axial nodes down the prothorax is known to vary amongst species of *Olenellus*: the nodes may be present on every segment (e.g. on the neotype of *O. thompsoni* (Hall, 1859)), or be present only on just a subset of segments (e.g. on the lectotype of *O. transitans* (Walcott, 1910)) (see also Palmer 1998, p. 667). (This variation amongst *Olenellus* species was acknowledged by Lieberman [1998, p. 78], but deemed to be inconsequential for the broad phylogenetic analysis presented therein. The distribution of prothoracic axial nodes was not included as a character in a subsequent cladistic analysis of species within the genus *Olenellus* [Lieberman 1999]). Palmer (1998) subsequently mentioned intraspecific variation in the distribution of prothoracic axial nodes in *O. gilberti*, *O. chiefensis* and *O. terminatus* from the Ruin Wash Lagerstätte.

Variation in the distribution of prothoracic axial nodes amongst morphologically mature specimens of *O. gilberti* from the Ruin Wash Lagerstätte is graphically illustrated in Fig. 43B. The variation in distribution of prothoracic axial nodes is statistically indistinguishable for specimens in early phase 5 of cephalic development (Fig. 43A). Axial nodes are invariably present on T11 to T14, and invariably absent on T3 to T5. The run of consecutive prothoracic segments bearing an axial node variably begins at T6, T7, T8, T9, T10 or T11. Axial nodes typically progressively increase in size on these consecutive segments (being largest on more posterior segments), and are sometimes developed only as subtle swellings on the anterior one, two, three or four segments of the run. (Palmer [1998, p. 667] noted that the run of segments bearing an axial node sometimes begins at T12. This observation might have been drawn from a specimen that was not
examined herein, or it is possible that a subtle swelling on T11 was overlooked.) An axial node is variably present or absent on T1. Development of an axial node on T2 is also variable. Presence of a node on T2 is consistently associated with presence of a node on T1, but presence of a node on T1 is not consistently associated with development of a node on T2. Development of an axial node on T1 (or T1 and T2) is apparently independent of the distribution of nodes on more posterior prothoracic segments. The most commonly observed conditions were the presence of axial nodes on T9 or T10 to T14 only. This documentation of the range of intraspecific variation in prothoracic axial node distribution within a single collection of *O. gilberti* provides an empirical baseline that will be useful in determining whether differences in axial node distribution amongst other, less thoroughly sampled *Olenella* morphotypes represent interspecific disparity or intraspecific variation. Potential developmental controls on the distribution and size of prothoracic axial rings are discussed below.

**Opisthothorax.** Completely articulated specimens of olenellid trilobites are rare, and the total number of thoracic segments is known for very few species. Several fully articulated specimens of *Olenella gilberti* have been recovered from the Ruin Wash Lagerstätte. Four such specimens were examined herein. One specimen (sagittal cephalic length 18.67 mm; Figs 14A, 15A) possesses two opisthothoracic segments. A slightly smaller specimen (sagittal cephalic length 15.67 mm; Figs 14B, 15B) possesses at least three and perhaps more opisthothoracic segments (the number being uncertain because the details are obscured by the large axial spine of T15). Larger specimens possess three opisthothoracic segments (sagittal cephalic length 18.82 mm, Figs 14D, 15D; sagittal cephalic length 24.25 mm, Figs 14C, 15C). Palmer (1998, p. 667) noted that the *O. gilberti* opisthothorax bore up to four segments, a count that lies beyond the definite range seen on specimens from Ruin Wash examined herein. The present author collected a specimen of *O. gilberti* from the Cadiz Formation (Marble Mountains, California) that bears either three or four opisthothoracic segments (the number again being uncertain due to obstruction by the large axial spine of T15), and the pygidium is not preserved, so the total number may have been even greater. That specimen has a sagittal cephalic length of approximately 12.27 mm.

*Olenella gilberti* therefore exhibited intraspecific variation in the number of opisthothoracic segments, with totals ranging from two to at least four. This variation is expressed amongst specimens collected from a very narrow stratigraphical interval at a single site (the Ruin Wash Lagerstätte). The specimens upon which counts of opisthothoracic segment number were made are all of mature cephalic morphology (late phase 5 of development), and the number of opisthothoracic segments does not consistently correlate with cephalic size. Large individuals, despite presumably being older and having passed through more moults, sometimes possess fewer opisthothoracic segments than smaller individuals. Variation in segment number therefore cannot be simply attributed to variation in size (age) of the individuals.

**Discussion**

**Phylogenetic affinities of *Olenella gilberti***

The generic assignment of *O. gilberti* is not contentious (Palmer 1998). However, phylogenetic relationships amongst the many (more than 50 named) species of *Olenella*, and in particular the placement of *O. gilberti*, are less clear. Palmer & Repina (1993; Palmer & Repina in Whittington et al. 1997) recognized five subgenera within *Olenella*, and Palmer (1998) assigned *O. gilberti* to *Olenella* (*Olenella*). However, Lieberman (1998, 1999) raised two of those five subgenera to generic status (as...
Mesolenellus Palmer & Repina, 1993 and Mesonacis), recognized Olenellus (Angustiolellus) Palmer & Repina, 1993 as a junior synonym of Olenellus, and Olenellus (Paedeumias) Walcott, 1910, preferring instead to abandon subgeneric assignments within Olenellus. Olenellus gilberti was not included in Lieberman’s (1998, 1999) cladistic analyses. Palmer (1998, p. 668) noted that the thorax of O. gilberti is “not clearly distinguishable” from that of O. getzi Dunbar, 1925, a species that differs from O. gilberti in possession of a deeper ocular furrow and a larger intergenal spine that is located closer to the base of the genal spine at morphological maturity. Lieberman’s (1999) cladistic analysis supported a sister-species relationship between O. getzi and O. crassimarginatus (Walcott, 1910), with O. robsonensis (Burling, 1916) and O. thompsoni as progressively more basal outgroups. Phenetically, O. gilberti is very similar to the stratigraphically older Olenellus n. sp. (“Olenellus aff. gilberti A” of Webster et al. 2003; “Olenellus n. sp. 3” of Webster 2011b; see above), from which it differs by lacking a distinct intergenal spine at morphological maturity. Another new species of Olenellus from the Eager Formation near Cranbrook, British Columbia (“Olenellus gilberti” of Best 1952; Hu 1985) is also similar to O. gilberti s.s., but differs in possessing a relatively narrower cephalic border, proportionally shorter ocular lobes, in the location of the intergenal spine/node along the posterior cephalic margin, and in the distribution prothoracic axial nodes (see Palmer 1998). Neither of these species was included in Lieberman’s (1999) cladistic analysis. The phylogenetic relationships amongst all these species will be investigated in a forthcoming cladistic analysis.

Comparative ontogeny
In the 136 years since the first description of the ontogeny of an olenelloid trilobite (Ford 1877), morphologically immature specimens of more than 60 other olenelloid species have been illustrated. Detailed, quantitative accounts of cephalic development have been provided for Olenellus puertoblancoensis (Lochman in Cooper et al., 1952) and Olenellus aff. fowleri (see Palmer 1957 [as Paedeumias clarki Resser, 1928 and O. gilberti, respectively]), and for Nephrolenellus multinosus and N. geniculatus (see Webster 2007b). Silicified ontogenies have also been illustrated (but with only cursory description) for Bristolia anteros and B. fragilis (see Palmer & Halley 1979). Such studies provide a wealth of data to which the ontogeny of O. gilberti can be compared. To date, ontogenetic data have not been taken into account in studies of olenelloid phylogeny (Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Lieberman 1998, 1999). The discussion below (also Table 6) highlights several features of olenelloid ontogeny that are potentially phylogenetically informative and will be utilized in future cladistic analyses of the group.

The cephalon of O. gilberti passed through the same five phases of development that have been recognized in other olenelloids (see above). However, some taxa (e.g. N. multinosus and N. geniculatus, also B. anteros) terminate development in phase 4. Entry into phase 5 of cephalic development is defined by the onset of pronounced proportional lateral widening of L2 (so that the glabella became transversely narrowest at S1), and is often associated with the distal merger of L2 with L3 and the corresponding isolation of S2 from the axial furrow. The distal merger of L2 + L3 (e.g. character 31, state 1 of Lieberman 1998) is contingent upon entering phase 5 and is thus always associated with anterior divergence of the lateral margins of L2 (e.g. character 35, state 1 of Lieberman 1998; mis-coded for the effaced taxon Biceratops nevadensis Pack & Gayle, 1971). Such non-independence of character state combinations can be overlooked without consideration of ontogeny.

The ocular lobes and glabella oncephala of O. gilberti in early phases of development have rather subdued relief and are defined only by very shallow furrows (Figs 19, 20). Glabellar furrows did not become evident until mid-to late phase 3 of development (Figs 20, 21). In these regards, O. gilberti is very similar to O. puertoblancoensis

### Table 6. Ontogenetic characters that might prove to be phylogenetically informative.

| Species                  | Terminal phase of cephalic dev. | Ocular lobe relief | Dorsal expression of glabellar seg. | Interoc. furrows | Interoc. nodes | Glabellar axial nodes anterior to LO | Procr. spines | Ventral opening on intergenal spines |
|--------------------------|---------------------------------|-------------------|-------------------------------------|------------------|---------------|-------------------------------------|---------------|-----------------------------------|
| O. gilberti              | 5                               | low               | not expressed                       | absent           | absent        | absent                              | absent        | narrow                            |
| O. puertoblancoensis     | 5                               | low               | not expressed                       | absent           | absent        | absent                              | absent        | narrow                            |
| O. aff. fowleri          | 5                               | high              | expressed                           | present          | present       | present                             | absent        | wide                              |
| B. anteros              | 4                               | high              | expressed                           | present          | present       | present                             | present       | wide                              |
| B. fragilis              | 5                               | high              | expressed                           | present          | present       | present                             | absent        | wide                              |
| N. multinosus            | 4                               | high              | expressed                           | present          | present       | present                             | absent        | wide                              |
| N. geniculatus           | 4                               | high              | expressed                           | present          | present       | present                             | absent        | wide                              |

Abbreviations: O., Olenellus; B., Bristolia; N., Nephrolenellus; dev., development; Interoc., interocular.; Procr., procranial; seg., segmentation.
(Palmer 1957; Webster 2011c). Conversely, other olenelloids possess ocular lobes of far greater dorsal relief, have ocular lobes and glabella clearly defined by deep furrows, and exhibit clear glabellar segmentation at these early developmental stages (Table 6): examples include the two Nephrolenellus species (Webster 2007b), Para-nephrolenellus besti Webster, 2007c, B. anteros and B. fragilis (Palmer & Halley 1979), and O. aff. fowleri (Palmer 1957; Webster 2011c).

The interocular area of pre-phase 3 cephala of O. gilberti and O. puertoblancoensis is smooth, whereas the interocular area of pre-phase 3 cephala of the two Nephrolenellus species (Webster 2007b), B. anteros (Palmer & Halley 1979), and O. aff. fowleri (Palmer 1957; Webster 2011c) bears clear interocular furrows and interocular nodes (Table 6). Amongst the taxa listed in Table 6, the presence of interocular nodes is always associated with the presence of interocular furrows. There is no obvious a priori reason to assume that these characters are dependent, although proving this will require discovery of a species that bears interocular furrows and lacks interocular nodes (or vice versa).

The glabella of pre-phase 3 cephala of O. gilberti lacks axial nodes on lobes anterior to LO, and in this respect is similar to O. puertoblancoensis, O. aff. fowleri, B. anteros and B. fragilis. Conversely, prominent glabellar axial nodes are developed anterior to LO on pre-phase 3 cephala of the two Nephrolenellus species (Table 6). These axial nodes are then progressively reduced in size and lost, anteriormost first, through subsequent ontogeny (Webster et al. 2001; Webster & Zelditch 2005; Webster 2007b).

Short procranidial spines are present on pre-phase 3 cephala of O. puertoblancoensis, O. aff. fowleri, B. anteros and B. fragilis, but are absent throughout ontogeny of O. gilberti and the two Nephrolenellus species (Table 6). The distribution of procranidial spines amongst the species listed in Table 6 is incongruent with the distribution of the other characters pertaining to cephala in phase 3 of development, implying that the spines were independently gained (or lost, depending on polarity) at least twice.

The intergenal spines on pre-phase 3 cephala of O. gilberti are thin and almost cylindrical in transverse cross section, bearing only a very narrow slit-like opening running down their length on the ventral surface (see above; Fig. 19U, V). Such a condition is also found on pre-phase 3 cephala of O. puertoblancoensis. However, the intergenal spines of pre-phase 3 cephala of the two Nephrolenellus species, B. anteros, B. fragilis and O. aff. fowleri are somewhat broader (tr.) and gutter-shaped in transverse cross section with a wide opening running down their length on the ventral surface (Table 6). Amongst the species listed in Table 6, the distribution of very narrow versus wide ventral openings on the intergenal spines is identical to the distribution on pre-phase 3 cephala of low versus high ocular lobe relief, of non-expressed versus expressed glabellar segmentation, and of smooth versus furrow- and node-bearing interocular areas. Again, there is no obvious a priori reason to assume that any of these characters should be functionally or developmentally required to covary, but unequivocal demonstration of their independence will require discovery of taxa showing novel state combinations.

**Instar number and homology.** Olenellus gilberti apparently passed through four instars prior to entry to phase 3 of cephalic development (above). Distinct size-clusters of specimens, interpreted to represent instars, have been previously identified in two olenelloid species: O. puertoblancoensis (see Palmer 1957, text-fig. 5; misidentified as Paedeumias clarki) and Nephrolenellus multinodus (see Webster 2007b, fig. 2.3). Poulsen (1974) also identified putative instars in Mesolenellus hyperborea (Poulsen, 1974), but these claims were not supported by subsequent statistical investigation (Hunt & Chapman 2001; although see above for demonstration of the sensitivity of such statistical methods to deviations from non-normal data distribution within instars). Both O. puertoblancoensis and N. multinodus passed through five instars prior to entering phase 3 of cephalic development (Palmer 1957; Webster 2007b). How can we account for the difference in pre-phase 3 instar number between O. gilberti and these other species?

The five sampled instars of O. gilberti might be developmentally homologous (e.g. in terms of number of moulting events since a standard developmental event such as hatching or entry into the meraspid period) to the five sampled instars of O. aff. fowleri and of N. multinodus (Table 7). Under this hypothesis, for any given sampled instar in their respective ontogenies, the mean sagittal cephalic length of O. gilberti consistently exceeds that of O. aff. fowleri, and the value for both of those

| Instar | O. gilberti (this study) | O. aff. fowleri (Palmer, 1957)* | N. multinodus (Webster, 2007b) |
|--------|--------------------------|--------------------------------|-------------------------------|
| 1      | 0.61                     | 0.57                           | 0.49                          |
| 2      | 0.75                     | 0.67                           | 0.60                          |
| 3      | 0.89                     | 0.77                           | 0.65                          |
| 4      | 1.08                     | 0.95                           | 0.76                          |
| 5      | 1.27                     | 1.16                           | 0.89                          |
| NLS    | 1.34                     | 1.26                           | 1.06                          |

Abbreviations: O., Olenellus; N., Nephrolenellus; NLS, next largest sampled specimen (presumably belonging to instar 6).

*Palmer (1957) did not provide cephalic length values for this species.

Values of cephalic length in instars 1, 2, 3 and 5 for this species were therefore calculated from illustrations (Palmer 1957, text-fig. 6); cephalic length for instar 4 was estimated by interpolation so as to minimize the variance in growth ratio across all five instars.
species exceeds that of *N. multinodus* (Table 7). Genal spines (marking entry into phase 3 of cephalic development) first appear on the fifth sampled instar of *O. gilberti* (mean sagittal cephalic length = 1.27 mm), and the next largest specimens (presumably representing the sixth instar, although this is not represented as a distinct size-cluster) are 1.34 mm in sagittal cephalic length (Table 7). Genal spines first appear on specimens 1.26 mm in sagittal cephalic length of *O. aff. fowleri*, and 1.06 mm in sagittal cephalic length of *N. multinodus* (in both cases, presumably representing the sixth instar; Table 7). If the first five instars are deemed to be homologous across these three species, then (1) for each instar, the species consistently follow a size gradient of *O. gilberti* > *O. aff. fowleri* > *N. multinodus*; and (2) the onset of genal spine differentiation is pre-displaced in *O. gilberti* (instar 5) relative to the other two species (instar 6) (Table 7). This suggests phylogenetic and/or environmental lability in cephalic size and in the developmental timing of genal spine differentiation (a timing modification *sensu* Webster & Zelditch 2005).

However, it is notable that the sagittal cephalic length at which genal spines first appear is very similar for *O. gilberti* and *O. aff. fowleri*. It is therefore possible that the fifth sampled instar of *O. gilberti* is homologous to the sixth instar of *O. aff. fowleri*, and that the *k*th sampled instar of *O. gilberti* is homologous to the *k* + 1st sampled instar of the other species (Table 8). If so, then (1) the absolute magnitude of interspecific cephalic size differences is reduced for each instar, with a typical size gradient of *O. aff. fowleri* > *O. gilberti* > *N. multinodus* (except for putative instar 6); and (2) the hypothetical first instar of *O. gilberti* was not sampled in this study (compare Table 8 to Table 7). Given the large volume of rock dissolved and the high number of specimens recovered in the present study, it is deemed unlikely that specimens representing such a hypothetical first instar of *O. gilberti* were overlooked. Existence of the hypothetical first instar would therefore require that either (1) its exoskeleton was not calcified in life and did not become silicified; or (2) it lived elsewhere and only the second and subsequent instars inhabited the water column at this site. Calcification of the trilobite exoskeleton has been assumed to have coincided with hatching (e.g. Speyer & Chatterton 1990, fig. 8; although see Speyer & Chatterton 1990, fig. 1 and Chatterton & Speyer in Whittington et al. 1997, fig. 140 for a hypothetical decoupled situation). That assumption, if true, argues against the existence of an unmineralized free-swimming *O. gilberti* instar. However, timing modifications to the onset of exoskeletal calcification relative to events such as hatching and the first development of trunk articulation are inferred to have occurred in other trilobite clades (Speyer & Chatterton 1990; Chatterton & Speyer in Whittington et al. 1997, fig. 147; Park & Choi 2011), and it is possible that *O. gilberti* passed through the equivalent of the first instar prior to hatching. Indeed, it has been argued that delayed hatching/calcification characterizes the entire Olenellina because protaspides are entirely unknown within the group (Chatterton & Speyer in Whittington et al. 1997, p. 219).

Aspects of morphology other than cephalic size offer conflicting data towards the resolution of this issue of interspecific instar homology. The first sampled instar of *O. gilberti* most closely resembles the first sampled instar of *O. aff. fowleri*, because both possess ocular lobes that extend to the lateral cephalic margin and thus truncate the cephalic border (compare Fig. 19A, C to Palmer 1957, pl. 19, fig. 1). This trait therefore supports the instar homology outlined in Table 7. However, the fourth sampled instar of *O. gilberti* closely resembles the fifth instar of *O. aff. fowleri*, because both possess an extraocular area that extends to the posterior tip of the ocular lobe (compare Fig. 19Q, S to Palmer 1957, text-fig. 6, specimen at centre-right). This trait therefore supports the instar homology outlined in Table 8. Comparison of other traits between *O. gilberti* and *N. multinodus* is equally ambiguous. The transition from the first to the second sampled instar of *O. gilberti* is associated with a slight proportional increase in the distance between the intergenal spine bases relative to sagittal cephalic length (Fig. 16A). In *N. multinodus* the transition from the first to the second sampled instar is associated with a slight proportional decrease in this ratio; the ratio remains roughly constant from the second to the third sampled instar, and then increases between subsequent instar transitions during phase 2 of cephalic development (Webster 2007b, fig. 2.1). This trait therefore does not support the instar homology outlined in Table 7, but neither does it strongly support that outlined in Table 8.

| Instar | *O. gilberti* (this study) | *O. aff. fowleri* (Palmer, 1957)* | *N. multinodus* (Webster, 2007b) |
|--------|---------------------------|----------------------------------|---------------------------------|
| 1      | not sampled               | 0.57                             | 0.49                            |
| 2      | 0.61                      | 0.67                             | 0.60                            |
| 3      | 0.75                      | 0.77                             | 0.65                            |
| 4      | 0.89                      | 0.95                             | 0.76                            |
| 5      | 1.08                      | 1.16                             | 0.89                            |
| NLS    | 1.27                      | 1.26                             | 1.06                            |

Abbreviations: *O.* *Olenellus*; *N.* *Nephrolenellus*; NLS, next largest sampled specimen (presumably belonging to instar 6).

*Palmer (1957) did not provide cephalic length values for this species. Values of cephalic length in instars 1, 2, 3 and 5 for this species were therefore calculated from illustrations (Palmer 1957, text-fig. 6); cephalic length for instar 4 was estimated by interpolation so as to minimize the variance in growth ratio across all five instars.

Table 8. Alternative homology of sampled instars across three species of olenelloid trilobites. Grey shading indicates presence of genal spines.
Broader phylogenetic and geographical sampling of ontogenies is necessary to test these various hypotheses of instar homology and of developmental timing modifications. Nevertheless, it is clear that considerable evolutionary lability existed in cephalic size and timing of developmental events such as exoskeletal mineralization and/or genal spine differentiation even during early ontogenetic stages of these olenelloids. This observation is congruent with the apparent phylogenetic lability of procranial spine development on pre-phase 3 cephalas (above).

Intraspecific variation
As documented above, *Olenellus gilberti* exhibits variation in many traits even when controlling for preservational mode and ontogeny. Amongst morphologically mature specimens (in late phase 5 of cephalic development) there is variation in many quantitative aspects of cephalic shape (e.g. Figs 4, 5, 42), in many qualitative aspects of cephalic morphology (e.g. presence or absence of extraocular genal caeca, an anterior ocular line, an intergenicral ridge, a genal ridge and a posterior ocular line), in the distribution of prothoracic axial nodes (Fig. 43B), and in trunk segment number. Documentation of the frequency and magnitude of intraspecific variation in such traits is important for several reasons.

Firstly, the condition of many of these traits has been assumed to be phylogenetically informative within the Olenelloidea, and differences in such traits are used in species and clade delimitation (e.g. Palmer & Repina 1993; Palmer & Repina in Whittington et al. 1997; Palmer 1998; Lieberman 1998, 1999). A species should only be recognized when it is uniquely diagnosable from all others (in the condition of at least one trait or by a unique combination of conditions for several traits; Nixon & Wheeler 1990; Wheeler & Platnick in Wheeler & Meier 2000). The case for interpreting morphological differences between samples as interspecific disparity is therefore made stronger if it can be demonstrated that the difference exceeds the magnitude of intra-sample variation. The present study provides an empirical baseline of intra-sample variation in a wide range of traits (above) that can be used to guide interpretation of morphological differences amongst less well sampled putative species. Furthermore, knowledge and quantification of the magnitude of intraspecific variation in traits of phylogenetic significance can lead to better-informed decisions regarding character selection and coding in cladistic analyses, which can profoundly affect hypotheses of phylogenetic relationships (see Introduction for references). The present study will therefore help to resolve many of the long-standing problems regarding establishing robust diagnoses of and hypotheses of relationships amongst olenelloid taxa.

Secondly, the magnitude and structure of variation within a species can provide constraints on the rate and direction of phenotypic evolution, and can affect species survivorship on geological timescales (see Introduction for references). It will be of great interest to determine whether the structure of intraspecific variation (either ontogenetic or static) documented herein in any way parallels the pattern of phenotypic evolution within the clade as is predicted by, for example, the Kluge-Kerfoot phenomenon (e.g. Farris 1966, 1970; Kluge & Kerfoot 1973; Johnson & Mickevich 1977; Pierce & Mitton 1979; but see Sokal 1976 and Rohlf et al. 1983), or hypotheses of evolution by heterochrony (e.g. Gould 1977; Alberch et al. 1979; Webster & Zelditch 2005) or lines of least resistance (e.g. Schluter 1996; Hunt 2007). Such an investigation necessarily requires placement of *O. gilberti* within a defensible phylogenetic framework, and is therefore beyond the scope of the present study.

Controls on variation and implications for canalization of developmental processes in early trilobites. Previous claims of high levels of intraspecific variation in olenelline trilobites relative to more derived trilobites have led to a suggestion that developmental processes were less tightly canalized in early trilobites (McNamara 1986; see also Hughes 1991, 1994). The present study represents the most detailed exploration of the nature of phenotypic variation in an olenelline (and perhaps any) trilobite, and parses that variation into dynamic (ontogenetic), static and taphonomic components. Such detail provides some insight into the controls on the magnitude and structure of that variation, and thus offers an opportunity to test the hypothesis of weak canalization of development.

For each of phase 4, early phase 5 and late phase 5 of cephalic development, the dominant structure of static (size-standardized) cephalic shape variation closely parallels the pattern of ontogenetic shape change through that portion of ontogeny (above). This suggests that anatomical regions that covary in shape during ontogeny might also covary in shape when static (non-ontogenetic) variation alone is considered. If so, then a decoupling between size and the average trajectory of ontogenetic shape change would appear to be the source of much of the static (non-ontogenetic) shape variation within each phase of cephalic development, and intraspecific heterochrony may have been an important contributor to size-independent shape variation. This parallels the situation for intraspecific variation in cephalic shape of Cambrian ptychoparioid trilobites (Webster 2011a) and in thoracic segment number of Cambrian trilobites (see below). This would indicate that the structure of variation within early trilobite species was relatively tightly constrained by their respective patterns of ontogenetic phenotypic change. The hypothesis that developmental processes were less tightly canalized in early trilobites would then primarily
correspond to this decoupling of form from size, rather than referring to a general ‘sloppy development’ whereby growth in each trait was poorly constrained and essentially independent of all other traits. However, it is risky to apply biological meaning to an individual principal component, because the actual shape variation in a particular anatomical region is described by the net effect of all PCs on that region: PCs are mathematically independent descriptors of variation within a sample, but do not necessarily equate to biologically independent factors explaining that variation. More complex analytical techniques must be applied to meaningfully resolve the structure of integration amongst anatomical regions and to compare that to the structure of ontogenetic shape change within a species (e.g. Webster & Zelditch 2008, 2009, 2011a, b).

Pendling the application of such techniques to Olenellus gilberti, the above discussion must be considered speculative.

In both early and late phase 5 of cephalic development, O. gilberti exhibits variation in the distribution of axial nodes on the prothorax (above). Various authors have considered the developmental underpinning of variation/dispersity in trilobite axial node distribution. Sundberg (2000, p. 260) proposed that the transition from the absence of axial nodes on anterior thoracic segments to the presence of axial nodes on posterior thoracic segments, exemplified by O. chiefensis and O. terminatus, was indicative of the presence of two distinct ‘thoracic regions’, each perhaps under the control of a different (suite of) homeotic gene(s). Differences in the distribution of thoracic axial nodes amongst olenelloid species were interpreted as homeotic change (Sundberg 2000, p. 266), defined as “the transfer of a feature typical of one region or segment to another body region or segment” (Sundberg 2000, p. 258). Sundberg’s (2000) hypothesis of homeotic gene expression in trilobites was heavily critiqued by Hughes (2003), who presented a rather different hypothesis founded on recent advances in knowledge of Hox gene number and expression. Hughes (2003) convincingly argued that Sundberg’s (2000) supposed thoracic subdivisions were unrelated to trilobite tagmosis, and that (variation in) axial node distribution was unlikely to reflect (variation in) boundaries in Hox gene expression domains. Webster & Zelditch (2005) categorized evolutionary changes in axial node distribution as examples of heterometry (modification of the number of a particular morphological feature), but did not speculate on the genetic underpinnings of such changes. Recent work on spine development in modern arthropods may shed light on the proximal control over (variation in) node distribution. It has been demonstrated that the location and shape of beetle ‘horns’ is controlled by a limb-patterning pathway involving the distal-less (dll), wingless (wg) and decapentaplegic (dpp) genes, amongst others (Emlen et al. 2006). The ultimate size of the ‘horn’ is influenced by expression domains of the patterning genes, by the relative size of molecularly distinct epithelial domains within the growing ‘horn’ primordium, and by the nutritional condition of the individual (coupled to cell proliferation rate via the insulin pathway) (Emlen 1997; Emlen et al. 2006). It is therefore plausible that intraspecific variation and interspecific disparity in the axial node/spinelet/spine distribution of trilobites was driven by changes in the expression domains of patterning genes such as dll, wg and dpp.

(That is not to say, of course, that trilobite axial nodes/spinelets/spines were under strong sexual selection, as the greatly exaggerated beetle ‘horns’ are, but only that the developmental pathways involved in the morphogenesis of axial extensions of the exoskeleton may be common to both). This putative developmental mechanism of phenotypic change in trilobites will be further explored in a future study (Webster & Emlen, in preparation). If such a hypothesis is supported, then the intraspecific variation in axial node distribution and size documented herein could reflect genetic and/or environmental (i.e. nutritional condition) differences amongst the individuals. In either case, it is clear that the developmental system of O. gilberti was not perfectly buffered against such genetic and/or environmental variation, so that the resulting phenotype was not perfectly canalized in axial node size and distribution.

Olenellus gilberti exhibits variation in thoracic (specifically opisthothoracic) segment number at morphological maturity that is not simply attributable to variation in size of the individuals (above). Intraspecific variation in thoracic segment number at morphological maturity was rare amongst trilobites (e.g. Hughes et al. 1999). Most documented cases involve Cambrian species (see table 1 in Hughes et al. 1999; this study). There are only two previously reported cases of variation in segment number amongst olenelloid trilobites. Whittington (1989) documented intraspecific variation within O. thompsoni (with 14 prothoracic segments and variably four or five opisthothoracic segments). However, this purported case is complicated by an overly inclusive concept of O. thompsoni adopted by Whittington (1989; see more recent systematic revisions by Lieberman 1998, 1999): the degree of variation exhibited by O. thompsoni as currently understood is presently under investigation. Geyer (1993; not listed by Hughes et al. 1999; table 1) documented intraspecific variation in thoracic segment number (15 or 16) in the olenelloid trilobite Cambropallas telessto Geyer, 1993, a species in which the thorax was not differentiated into a prothorax and opisthothorax. Olenellus gilberti thus represents only the second unambiguous example of an olenelloid trilobite showing intraspecific variation in thoracic segment number.

It has been suggested that intraspecific variation in thoracic segment number might reflect weak canalization of morphology stemming from imperfectly regulated development systems (e.g. McNamara 1983, 1986). Others have argued that variation in thoracic segment number
may have been driven by ecological factors (Hughes et al. 1999). The present study is silent as to the cause of variation in segment number within *O. gilberti*. However, the observations demonstrate that the developmental system of *O. gilberti* was not perfectly buffered against internal or external sources of variation in segment number.

As noted above, the fact that the variance in two log-transformed measures of cephalic size fails to increase (and actually decreases for the distance between the intergenal spine bases) from instars 1 to 5 (Fig. 16E, F) is consistent with either (1) targeted growth; or (2) the existence of strong (and increasing) selection on two size variables during the early ontogenetic stages of an early Cambrian trilobite. The first interpretation implies tight regulation over growth and, if true, would provide a counterargument against the hypothesis that developmental systems of early Cambrian organisms were relatively poorly canalized. The second interpretation implies a steep decrease in fitness away from an optimum phenotype, perhaps related to food-gathering capability, to the ability to avoid predators, and/or to locomotory efficiency. The magnitude of selective pressure relating to competition amongst individuals in early Cambrian communities (either for a limited resource or in predator/prey relationships) might prove impossible to quantify, although was unlikely to have exceeded that in modern communities (see papers in Zhuravlev & Riding 2001). However, it might be possible to experimentally determine the functional performance of larval traits relating to locomotion in the water column (e.g. the effect of body size or spine separation on buoyancy), and thus test whether ontogenetic trends in trait variance (Fig. 16E, F) are consistent with biomechanical/functional constraints.

It is also demonstrated above that cephalic shape variation is constant (at 95% confidence) from phase 4 to late phase 5 of cephalic development (Fig. 38). This pattern is consistent with the results of the study of cephalic size variation over instars 1 to 5 and, like for that analysis, the two alternative explanations cannot be unambiguously distinguished without longitudinal data or knowledge of death selectivity. These results therefore provide evidence either (1) against a hypothesis of poor canalization of developmental systems in early Cambrian organisms; or (2) for the existence of a steep decrease in fitness away from an optimum phenotype.

It is intriguing that *O. gilberti* exhibited variation in traits such as prothoracic axial node distribution and thoracic segment number at morphological maturity, while variation in traits such as cephalic size and shape appears to have been constant or even to have declined through ontogeny. A similar pattern holds for the Silurian trilobite *Aulacopleura konincki*, which exhibited 18 to 22 thoracic segments at maturity but a constant degree of variance in size through meraspid development (Fusco et al. 2004). If the pattern of constant or decreasing variance in size and shape through ontogeny resulted from targeted growth rather than selective deaths (see above), then both *O. gilberti* and *A. konincki* demonstrate that flexibility in traits such as thoracic segment number need not be indicative of general ‘sloppiness’ in overall development (see also Hughes 2005, p. 154).

**Was the degree of variation exhibited by *Olenellus gilberti* high compared to other trilobites?** There is ample theoretical and empirical support for the hypothesis that the rate and direction of phenotypic evolution within a clade is governed, in part and at least over short evolutionary timescales, by the amount and structure of phenotypic variation within and amongst its constituent species (see references in Introduction). However, relatively few studies have explored whether there is a long-term (millions of years) trend in the level of intraspecific variation in particular traits, and how any such trends affected clade diversification over long evolutionary timescales. It has been suggested that there is ‘a general tendency for evolution to go from variation to fixation’ (termed ‘Rosa’s rule’ by Ramskold 1991). Support for such a tendency has been levied from studies of mature thoracic segment number in trilobites. This trait varies amongst congeneric species or even intraspecifically in several Cambrian clades, but is often invariable at much more inclusive levels of phylogenetic inclusivity amongst post-Cambrian clades (e.g. Jaanusson 1975; Hughes et al. 1999). Several authors have commented upon the temporal coincidence between the peak frequencies of intraspecific variation and phylogenetic change in thoracic segment number (e.g. McNamara 1983, 1986; Hughes et al. 1999; Hughes 2005; Webster 2007a). This has led to speculation that weak developmental canalization of this trait was permissive of its rapid evolutionary disparification in early trilobites, and that the subsequent decline in phylogenetic lability of this trait resulted from a progressive increase in its developmental canalization (McNamara 1986; see also Hughes 1991, 1994). (Of course, increasing constraints imposed by temporal change in ecological factors, e.g. increasing competition and incumbency, might also account for some or all of this pattern.) The variation in mature thoracic segment number documented here within *O. gilberti* strengthens the case for imperfect canalization of this trait in early trilobites. But the rapid morphological diversification of trilobites during the Cambrian involved evolutionary lability in many more traits than just thoracic segment number. Did early trilobite species, including *O. gilberti*, also exhibit higher levels of intraspecific variation relative to later trilobites in other traits?

This question cannot easily be addressed in terms of quantitative comparison of shape variation across taxa because high disparity amongst clades limits the applicability of many morphometric approaches: the cephalic landmark configurations used herein, for example, cannot
often be applied to non-olenelline trilobites because the cephalon of those trilobites is rarely preserved intact, being dissected from the cranidium and librigenae by facial sutures. Furthermore, the ontogeny and variation of very few (if any) other trilobites have been studied in as much detail as has now been done for \textit{O. gilberti}, thus limiting the scope for comparison. For example, data pertaining to patterns of shape or size variation through ontogeny are simply too sparse to determine whether the pattern seen in \textit{O. gilberti} (consistent with targeted growth) is atypical. (But the interpretation of such a pattern as having resulted from targeted growth is certainly inconsistent with the hypothesis of weakly canalized development in an early trilobite.) That Fusco \textit{et al.} (2004) documented a similar pattern in the Silurian trilobite \textit{A. konincki} is intriguing, but broad evolutionary generalizations should not be made from a sample size of two species.

Intraspecific variation in both shape and qualitative features has been studied in detail for the upper Cambrian dikeloccephalid trilobite \textit{Dikeloccephalus minnesotensis} Owen, 1852 (Hughes 1991, 1994). Like \textit{O. gilberti}, \textit{D. minnesotensis} showed static (non-ontogenetic) variation within single samples in the prominence of caeca, the distribution of terrace lines on the cephalon, the prominence of glabellar pustulation, the presence/absence of an occipital tubercle, and possibly also thoracic segment number. (The latter species also exhibited variation in many other traits, including aspects of shape, that have no homologues in, and/or cannot be easily compared to, \textit{O. gilberti}.) Hughes (1991) compared the degree of variation within \textit{D. minnesotensis} to that of the Devonian trilobite \textit{Phacops rana} (Green, 1832) (now \textit{Eldredgeops rana}), and concluded that the former was far more variable than the latter. This again is suggestive of weaker canalization of traits in Cambrian trilobites. However, an ongoing investigation using more refined techniques suggests that \textit{\textit{D. minnesotensis} sensu} Hughes (1991, 1994) might in fact represent two or more species (N. C. Hughes, pers. comm., October 2012). The degree of variation within these species is still believed to be high (N. C. Hughes, pers. comm., October 2012), but is presumably less than originally documented for \textit{\textit{D. minnesotensis}} by Hughes (1991, 1994).

An alternative approach that permits comparison of intraspecific variation across many species is to focus on qualitative or meristic variation in traits that are homologous across many trilobite clades. This approach was adopted by Webster (2007a) who found, through a meta-analysis of cladistic character–taxon matrices, that the frequency and extent of intraspecific polymorphism (representing intraspecific variation within an evolving trait) was higher amongst the stratigraphically old and/or phylogenetically basal taxa relative to younger and/or more derived taxa. One such trait is thoracic segment number at maturity. Variation in this trait is known in fewer than 30 species, the vast majority of which are Cambrian in age (Hughes \textit{et al.} 1999; above). \textit{Olenellus gilberti}, which was not included in the meta-analysis, can therefore be added to a very short list of trilobite species exhibiting variation in this trait.

Variation in the presence versus absence of aspects of cephalic ornamentation was also explored by Webster (2007a, fig. S6). Again, intraspecific variation was extremely rare, being documented in only 29 of 816 species (3.6%) for which appropriate data were available. All but one of the species exhibiting such variation was of early or middle Cambrian age (the exception being a Late Ordovician phacopid; \textit{D. minnesotensis} was not included in the meta-analysis). \textit{Olenellus gilberti} exhibited variation in the presence/absence of many aspects of cephalic ornamentation at maturity, including Bertillon markings and extraocular genal caeca (above). These types of ornament were developed in many trilobite clades, and their variable expression in \textit{O. gilberti} (and other olenellloid species; Webster 2007b, c, 2009a) seems to be unusual on a broader phylogenetic scale. \textit{Olenellus gilberti} was also variable in terms of the spatial extent of Bertillon marking development on the glabella and ocular lobes (see above; Figs 7D, 9A, B, D, 11F). Ornament within other trilobites species was often far less variable in its spatial extent of development. Indeed, relatively subtle differences in the spatial extent of cephalic ornament is sometimes used to differentiate species (e.g. Waisfeld \textit{et al.} 2011, fig. 6).

In summary, \textit{O. gilberti} seems to have exhibited intraspecific variation at morphological maturity in many traits that were typically invariably expressed in other trilobite species. Data for morphologically mature \textit{O. gilberti} were herein drawn from specimens recovered from a very narrow stratigraphical interval at a single locality. The degree of intraspecific variation would presumably only increase if geographical and/or stratigraphical variation were studied. Of the few other species in which variation in those traits has been documented, most are also Cambrian in age. This supports the hypothesis that development of those traits was relatively weakly canalized in early trilobites. However, \textit{O. gilberti} also exhibited a pattern of variation in cephalic size and shape through ontogeny that is consistent with (but not necessarily diagnostic of) targeted growth. If such an interpretation is correct, then at least some aspects of morphogenesis in this early trilobite were remarkably well regulated. This highlights the complex and mosaic nature of both development and evolution, and cautions against generalizing observations from a limited number of traits to the entire organism.

**Autecology**

**Life mode.** Like other olenelloids, mature individuals of \textit{Olenellus gilberti} lack morphological adaptations for life in the nekton or plankton (e.g. Fortey & Owens 1990a, b;
Hughes 2001) and were surely primarily benthic. However, the ventral orientation of the intergenal spines on the smallest instar (Fig. 19B, E) would presumably have hampered locomotion on the seafloor, and those instars may therefore have spent much or all of their time in the water column. (See Zhang & Pratt [1999, p. 127] for a similar suggestion that ventrally orientated spines on a redlichine trilobite larva are indicative of a planktonic life mode.) The progressive rotation of the intergenal spines into an orientation that is more coplanar with the rest of the cephalon over the second to fifth instars (Figs 19H, J, O, R, 20F, H) suggests that the species transitioned to a benthic life mode during the meraspid period. In O. gilberti this inferred transition from a planktonic to a benthic life mode was not associated with a radical metamorphosis, unlike in many other trilobite species (Chatterton & Speyer in Whittington et al. 1997, pp. 197–198).

**Moulting.** Some articulated specimens of *Olenellus gilberti* are preserved in a distinctive arrangement whereby the rostral plate and hypostome (when visible) are located below the prothorax in an inverted attitude (ventral side up) and posteriorly pointing orientation, apparently having rotated by 180° relative to their life position (pivoting around the point of contact between the posterior corners of the rostral plate and the cephalic doublure near the base of the genal spines) (Figs 10A, 11D, 33C). Such a sclerite arrangement has been documented in *N. geniculatus* (Webster 2007b, figs 12.1, 14.4, 14.5). A specimen representing either *O. roddyi* Resser & Howell, 1938 or *O. getzi* displaying the same arrangement of the cephalon, rostral plate, and hypostome (albeit without the thorax) has been illustrated by several authors (e.g. Walcott 1910, pl. 34, fig. 6, as “Paedeumias transitans”; Poulsen 1927, fig. 7; Resser & Howell 1938, pl. 9, fig. 6, as “Paedeumias yorkeense”; Hupé 1952, fig. 18.3; Hupé 1953, fig. 48.3; see Lieberman (1999) for most recent taxonomic revision). Specimens with such a sclerite configuration are interpreted as exuvia (Stormer 1941; Hupé 1952, 1953; Henningsmoen 1975; Webster 2007b; but see Harrington in Harrington et al. 1959, p. 0114 for a dissenting view). The peculiar arrangement of sclerites can be explained in terms of inferred moulting behaviour.

Olenelloids lack a facial suture, and during ecdysis the trilobite must have egressed anteriorly through the space between the cephalon and rostral plate (created by the opening of the marginal suture). The process of ecdysis probably involved dorsal arching of the body so that the median anterior edge of the rostral plate was braced against the substrate, in a manner similar to that described by Whittington (1990, figs 2–6) for *Paradoxides* Brongniart, 1822. Anteriorly directed pressure induced by the animal shuffling forwards would then have assisted in opening the marginal suture. Anterior egression of the animal would have dragged the dorsal exoskeleton forwards over the rostral plate, which would have swung into an increasingly vertical and downward-pointing orientation as it pivoted around its points of contact with the substrate and with the cephalic doublure near the base of the genal spines. The hypostome, which was conterminant with the rostral plate in some olenelloid species and was attached to the rostral plate by a hypostomal stalk in others, would have similarly rotated into a downward-pointing orientation. As anterior egression continued (or if the empty exuvium collapsed anteriorly through its own weight, through current action, or during burial), the rostral plate and hypostome (plus surrounding ventral integument) could have flipped entirely over about this pivot point, and thus come to lie in an inverted and posteriorly directed orientation relative to the dorsal sclerites of the exuvium (Figs 10A, 11D, 33C).

Most specimens showing this ecdysial configuration also show a disarticulation at the cephalon–trunk boundary, with the trunk being displaced anteriorly beneath the posterior portion of the cephalon (Figs 10A, 11D, 33C). This telescoping is consistent with the trunk of the old exoskeleton being tugged anteriorly as the animal egressed forwards through the space created by the opening of the cephalic marginal suture, the contact between the cephalon and first thoracic segment apparently being a site prone to disarticulation. On some specimens that exhibit such thoracic telescoping the rostral plate and hypostome are preserved close to life position (Figs 11E, 12B, 32B, 33E), and on others the position of the ventral sclerites is unknown. Whether these specimens also represent exuvia (with the ventral sclerites, when preserved, having undergone less extreme rotation, or with the exuvium having collapsed posteriorly following egression) is uncertain.

**Conclusions**

Consideration of ontogeny and intraspecific variation is critical for systematic palaeontology and can profoundly affect hypotheses of phylogenetic relationship amongst taxa. It is also crucial to our understanding of evolution, because the magnitude and structure of intraspecific variation (including phenotypic change during ontogeny) can constrain the rate and direction of phenotypic evolution. The need to document such variation is magnified for olenelline trilobites given their pivotal phylogenetic placement at the base of the Trilobita and the well-known difficulty in establishing robust diagnoses of, and hypotheses of relationship amongst, olenelline species and higher taxa. Previous claims that olenellines exhibited a high degree of intraspecific variation relative to more derived trilobites have been levied as support for a hypothesis that
Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*

1. The five successive phases of ontogenetic development of the cephalon that have been identified in other olenelloids are also applicable to *O. gilberti*. Quantitative analysis of shape variation using geometric morphometrics supports the distinction of these phases of cephalic development. The only differences are that (1) the change in the rate of transverse elongation of the posterior cephalic margin relative to increase in cephalic length that distinguishes phase 1 from phase 2 in other olenelloids is not detected, so that immature cephalon lacking genal spines can only be assigned to ‘pre-phase 3’ of development; and (2) the final phase of development (phase 5) is partitioned into ‘early’ and ‘late’ portions, differentiated by a subtle but significant change in allometric patterning of the glabella that has not yet been detected in other olenelloids. Specimens in late phase 5 of cephalic development (sagittal cephalic length > 9.3 mm) are considered to be morphologically mature.

2. Ontogenetically controlled comparison of non-compacted cephalon preserved in a silicified state with compacted, non-silicified cephalon preserved in shale reveals that taphonomic compaction caused a significant change in mean fossil form and an increase in shape variance. This demonstrates that many aspects of biological (pre-compactional) shape and shape variation (including ontogenetic shape change) are distorted and blurred by taphonomic compaction of fossils. Whether the magnitude of this compaction-related shape distortion is problematic to any investigation will depend on the nature of that investigation.

3. At morphological maturity, *O. gilberti* exhibited variation in many quantitative aspects of cephalic shape, in qualitative aspects of cephalic morphology (presence/absence of various anatomical features and the type and spatial extent of various ornaments), in the number, size, and distribution of prothoracic axial nodes, and in the number of opisthothoracic segments. This provides an empirical baseline of intra-sample variation that will be used to guide interpretation of morphological differences amongst less well sampled putative species, and will lead to better-informed decisions regarding character selection and coding in future cladistic analyses.

4. Comparative ontogeny reveals several features of development that have potential utility as informative characters for future phylogenetic analysis of olenelline trilobites. At least one of these traits (presence of procranidial spines on pre-phase 3 cephalon) was apparently phylogenetically labile and prone to homoplasy, being independently gained (or lost) at least twice.

5. Five instars are identified based on size-clustering: four within pre-phase 3 of cephalic development, and one representing the earliest instar of phase 3. Growth coefficients are biologically reasonable when compared to values for other trilobites. Two potential homology schemes of the four pre-phase 3 instars of *O. gilberti* with the five pre-phase 3 instars of other olenelloids are presented. Either would imply phylogenetic and/or environmental lability in cephalic size and in the developmental timing of some events (genal spine differentiation and/or exoskeletal mineralization).

6. Over instars 1 to 5, the variance of log-transformed cephalic length does not significantly change, and the variance of log-transformed intergenal spine separation significantly decreases. This pattern can be interpreted as either (1) the oldest known case of targeted growth in animal history; or (2) the existence of strong (and increasing) selection on two size variables during the early ontogenetic stages.

7. Counter to the common expectation of increasing variation through ontogeny, the magnitude of static cephalic shape variation does not significantly change from phase 3 to phase 4, from phase 4 to early phase 5 (based on silicified specimens), or from early to late phase 5 (based on non-silicified specimens). This suggests that either (1) cephalic shape variation was developmentally regulated; or (2) there was selection against deviant phenotypes through the later portions of ontogeny.

8. The dominant structure of static shape variation of the cephalon during each of phase 4, early phase 5 and late phase 5 is generally similar to the pattern of cephalic shape change during that portion of ontogeny. This parallelism suggests that intraspecific heterochrony (a decoupling between size and the average trajectory of ontogenetic shape change) might have been an important contributor to size-independent shape variation. However, the methodological basis for drawing this observation of parallelism is not well founded in biological terms, and the inference that the structure of
variation within early trilobite species was relatively tightly constrained by their respective patterns of ontogenetic phenotypic change must be considered speculative.

9. For many traits, the developmental system of *O. gilberti* was not perfectly buffered against internal and/or external variation, so that the resulting phenotype was not perfectly canalized in the condition of those traits (see conclusion 3, above). Intraspecific variation in such traits is rarely documented in later (especially post-Cambrian) trilobites, and is consistent with the claim that developmental systems of early trilobites were relatively poorly canalized.

10. Some data are consistent with (but not necessarily diagnostic of) tight regulation of some aspects of cephalic growth in *O. gilberti* (conclusions 6 and 7, above) and others indicate that the structure of shape variation in *O. gilberti* might have been constrained by ontogeny (conclusion 8, above). Such data are not indicative of general ‘sloppiness’ in development and, although open to other interpretations and thus not definitive in nature, should not be overlooked when considering the degree of canalization in early trilobites.

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Supplemental data

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