Abstract: Trilobites offer almost unparalleled insight into the growth and development of fossil ecdysozoans. Here I use newly collected material of *Elrathia kingii* (Meek) to estimate growth rates and describe shape change over the ontogeny of *E. kingii*. Well-preserved, articulated specimens from all post-embryonic stages were collected from a 1.5 m interval of the upper Wheeler Formation (Miaolingian Series, Cambrian) in western Utah (USA), and size and landmark-based shape data were digitized from photographs. Growth rates were estimated and compared with previously published data on the Silurian trilobite, *Aulacopleura koninckii* (Barrande). Like *A. koninckii*, the cephalic growth rate in *E. kingii* was constant and of similar magnitude to the minimum growth rate along the trunk, and growth rates in the trunk were lower during the holaspid ('adult') period than during the meraspid ('juvenile') period. However, body length at the onset of meraspis was smaller, the growth gradient along the trunk during meraspis was shallower, and the terminal number of thoracic tergites was smaller in *E. kingii* than in *A. koninckii*. Despite these differences, these two species had similar maximum body lengths, because higher overall growth rates in *E. kingii* compensated for other differences. The rate of cephalic shape change in *E. kingii* decreased at the transition from meraspis to holaspis, while the pygidium became more morphologically distinct from the thorax during holaspis. I also provide an emended diagnosis for *E. kingii*, descriptions of the ontogeny and ventral morphology, and evidence that *E. kingii* holaspids had an invariant number of tergites.

Key words: trilobite, growth rate, ontogeny, geometric morphometrics, Trilobita, Bolaspidella.

Knowledge of growth and development is critical to our understanding of evolution at the micro and macro scales (Moczek *et al.* 2015). Even though growth and development of extinct organisms must be inferred from fossilized remains rather than directly observed, the study of growth and ontogeny in fossil species can shed light on developmentally influenced evolutionary patterns and processes beyond what is possible from embryological studies alone (Urdy *et al.* 2013). In particular, differential growth rates determine body proportions and reflect the modular organization of organisms. Studying growth rates across the body throughout ontogeny requires large samples of specimens that preserve ontogenetic information. Among organisms that grow episodically, trilobites offer an unparalleled ontogenetic record: because they started biomineralizing their exoskeleton at early post-embryonic stages, the growth and morphological development of many species can be pieced together from samples that include fossilized exuviae as well as individual body fossils (Hopkins 2017).

As a result, there is a large body of literature describing ontogeny in trilobites (see also Chatterton & Speyer 1997; Hughes *et al.* 2006; Park & Choi 2011; and references within). Most of the work on growth rates, however, has focused on size increases in individual sclerites, in part because silification allows for the liberation of very small sclerites from a carbonate rock matrix but almost exclusively yields disarticulated material. Only one trilobite species, *Aulacopleura koninckii* (Barrande, 1846), has been the subject of studies where growth rates were estimated from a large collection of articulated specimens, with length measurements made from sclerites across the trilobite body at almost all stages of post-protaspis ontogeny (summarized in Hughes *et al.* 2017).

One of the most common and well-recognized trilobites in scientific, educational, and private collections is *Elrathia kingii* (Meek, 1870). Hundreds of thousands, if not millions, of specimens have been recovered from western Utah, USA, where the dominant mode of preservation consists of fibrous cone-in-cone calcite incrustations on the
ventral surface (Bright 1959; Gaines & Droser 2003; Robison et al. 2015), which help to retain the articulation of specimens even as they weather out of the surrounding matrix (Foster & Gaines 2016). Despite its ubiquity, *E. kingii* has been the subject of relatively little developmental or evolutionary biology research. A biometric analysis published by Robert Bright (1959) included a detailed assessment of growth rates of different sclerites measured from hundreds of specimens, but the sample consisted almost exclusively of holaspid specimens with the full complement of thoracic tergites (i.e. ‘adults’, see below for details). Although the holaspid exoskeletal morphology has been described in some detail (Meek 1870; Palmer 1954; Bright 1959; Robison 1964), only two meraspid specimens of this species have previously been figured (Bright 1959), and the ontogeny is otherwise undescribed. This study is the first to provide a detailed description of the ontogeny, including segmentation patterns and growth rates, of *E. kingii*. In addition, the analysis of growth rates was modelled after previous analysis of *A. koninckii* (Fusco et al. 2014, 2016), allowing for the first empirical comparison of body-wide growth rates in trilobite species.

**Segmentation in trilobites and its relationship to growth**

Like some centipedes and most crustaceans, the final segmental composition of the trilobite body was attained during post-embryonic ontogeny through a series of moults (Fusco & Minelli 2013). Trilobites had a hemi-anamorphic mode of segmentation, meaning that they underwent a phase of moults during which new segments were added to the body (anamorphosis) followed by a phase during which moulting continued without further increase in the number of body segments (epimorphosis; Minelli et al. 2003; Minelli & Fusco 2013). In trilobites, the earliest biomineralized moult is characterized by lacking articulation; this has been termed the protaspid period. The subsequent meraspid period began when moulting resulted in the first articulation between the cephalon and the trunk, each consisting of fused segments. During subsequent moults, either new segments were generated near the posterior end of the meraspid pygidium, or a new articulation appeared at the anterior end of the meraspid pygidium (i.e. a thoracic tergite was released into the thorax), or both. At some point, segment generation ceased (ending the anamorphic phase and initiating the epimorphic phase) and articulation generation ceased (ending the meraspid period and initiating the holaspis period). The relative timing of these transitions varied across species, and three different schedules have been documented in trilobites (Hughes et al. 2006). Both *Aulacopleura koninckii* and *Elrathia kingii* are interpreted to have been synantheromeric (Hughes et al. 2017; Systematic Palaeontology below), meaning individuals entered the epimorphic phase and holaspid period synchronously.

During the meraspid period, the number of tergites in the thorax is a size-independent measure of relative age of the individual. Per-moult size increase was constant for cephalia for some portions of the ontogeny in many trilobites (summarized by Chatterton & Speyer 1997; see also Fusco et al. 2004, 2012; Laibl et al. 2014), but studies of *Aulacopleura koninckii* indicate that the rate of growth in the thorax was governed by a growth field described by a continuous gradient rather than by constant per-tergite rates (Fusco et al. 2014, 2016). In these studies, this growth gradient along the trunk was best described by an exponential decay function, specifically that the growth at relative position $x$ along the trunk $= a + b \times \exp(-\lambda(1 - x))$, and shifted during the transition from meraspsis/ anamorphosis to holaspsis/epimorphosis.

**METHOD**

**Geological setting**

Specimens were collected from a 1.5 m-thick interval of thin-bedded mud limestone from the Wheeler Formation, c. 35 m below the base of the Marjum Formation, at North Antelope, in the House Range east of Dome Canyon, Millard County, Utah, USA (AMNH locality 3952). Other co-occurring trilobites included *Asaphus wheeleri* Meek, 1873, and *Bolaspidella housensis* (Walcott, 1886). No specimens of *A. wheeleri* with less than the terminal number of thoracic tergites (nine) were recovered, but many juveniles of *B. housensis* were, and the smallest stages can be difficult to distinguish from *E. kingii* (see Systematic Palaeontology). Based on the stratigraphic occurrence, the sampled interval is likely to represent the early *Bolaspidella* trilobite zone, latest Wuliuan or early Drumian (c. 504.5 Ma; Foster & Gaines 2016).

**Data collection**

Specimens were prepared from the matrix using a Swam Blaster® micro abrasive blaster (Crystal Mark). Specimens were then whitened with ammonium chloride vapour and photographed using a Canon 60D SLR camera and either a Canon EF 100 mm f/2.8 Macro IS USM or MP-e65 mm f/2.8 1–5× Macro lens on a Stackshot macro rail system (Cognisys); composite images were produced using Zerene Stacker (Zerene Systems). Sclerite lengths were measured from the photographs using ImageJ (Rasband 2018), either as length measurements for partially disarticulated specimens (Fig. 1A), or calculated as inter-
landmark distances (Fig. 1B). True tergite lengths are sometimes obscured along the sagittal axis because the occipital ring overlaps the axial ring of the first tergite and because not all specimens are perfectly prone. To circumvent this, the length of each tergite was estimated along both axial furrows and averaged. Summing across the lengths estimated in this way results in a slightly longer total body length compared with the distance measured from the anterior to posterior margins along the sagittal axis (Fig. 2), but the sets of sclerite lengths produced are more consistently comparable across specimens, where sclerites vary slightly in their relative orientation.

A total of 228 specimens were measured (Table 1; Hopkins 2020a), consisting of complete articulated (n = 170) and complete but partially disarticulated (n = 58) specimens, and representing holaspids (n = 152) and meraspids with four or more tergites (n = 76). Holaspid specimens are defined as having 13 thoracic tergites (see Systematic Palaeontology). Meraspid specimens were assigned to moult stages based on the number of tergites (e.g. moult stage M4 consists of specimens with four tergites). Specimens with fewer than four tergites were difficult to identify because of a co-occurring species that looks very similar in early ontogenetic stages (see Systematic Palaeontology), and so were excluded from the analysis.

Calculating growth rates

Cephalic growth rate was calculated using OLS regression of the natural log of cephalic length, i.e. ln(cephalic length), against meraspid moult stage (M4–M12, n = 76). To estimate the growth gradient along the trunk during the meraspid period, growth rates between stages were calculated by dividing the average tergite length in stage $i + 1$ by the average in stage $i$ for stages M4–M12 (n = 76). An exponential decay function was fitted to these growth rates against relative position in the trunk for each tergite at stage $i$.

Unlike meraspids, holaspids are characterized by having the same number of tergites, so this trait cannot be used as a size-independent measure of relative age. However, if it is assumed that the cephalic growth rate remains constant throughout ontogeny, holaspids can be assigned to moult stages by extrapolating from the OLS regression described above (Fusco et al. 2016). Once holaspid specimens have been assigned to moult stages, the growth gradient for the trunk during holaspis can be estimated following the same procedure as described above for meraspids. The highest moult stage is also an estimate of the largest number of moulting events that occurred for individuals within the species.

A function (par.est.R) for estimating the above parameters in the statistical programming language R (R Core Team 2019) is described in Hopkins (2020b). The procedure described above was followed to estimate growth rates and other parameters for Aulacopleura konincki, using data available from Hughes et al. (2017).

Cephalic shape change

Cephalic shape change was quantified using geometric morphometrics. Seventeen landmarks were chosen that represent the overall shape of the cranidium (Fig. 1B). Specimens that had more than three missing landmarks or were missing any pairs of landmarks were excluded. The symmetric component of variation for the remaining dataset (n = 160) was extracted following the Klingenberg et al. (2002) method for object symmetry using R

**FIG. 1.** Collection of shape and size data from Elrathia kingii specimens. A, example of length measurements taken from partially disarticulated specimen. AMNH-FI-115776. B, example of landmark data collected from articulated specimen. Only landmarks referenced elsewhere are numbered. AMNH-FI-115702. Scale bar is in mm.
functions from Haber (2015; see also Hopkins et al. 2016). Briefly, a mirror image is generated from each landmark configuration and then superimposed onto its original configuration and averaged, yielding a consensus configuration that is bilaterally symmetric for each specimen. All of the symmetric configurations were then superimposed jointly. In order to describe the amount of shape change occurring over ontogeny, the partial Procrustes distance between each specimen and the smallest specimen was calculated using the `procrdist` function from the R package `shapes v. 1.2.4` (Dryden 2018), and plotted against the natural log of centroid size. The presence and position of a shift in allometric growth was determined by fitting 12 models (one linear and 11 threshold models with breaks ranging from 1.1 to 2.0 ln centroid size). The best model was selected using the Akaike information criterion corrected for small sample size (AICc), and AICc weights were used to access the relative likelihood of each model (Burnham & Anderson 2002).

**RESULTS**

Total body length increased log-linearly over the meraspid period (Fig. 3), and per-moult range in body length was constrained during each meraspid moult stage to less than 1 mm. The transition from merasps/anamorphosis to holasps/epimorphosis occurred at c. 5 mm. Individuals continued to grow significantly during holaspis, with some individuals showing as much as a 7.5-fold increase in body length during the holaspis period.

Cephalic length increased log-linearly over the meraspid period (Fig. 4). The slope of the OLS regression indicates that the per-moult growth rate during the meraspid period was 1.12. Assuming that cephalic growth rates remained constant throughout the holaspis period, the largest *Elrathia kingii* required 28 moults to achieve a maximum body length of 3.6 cm (Fig. 5). If cephalic growth rates actually decreased during holaspis, then reaching these body lengths would have required an even larger number of moults. The OLS regression predicts that the

| No. thoracic tergites | Sample size |
|-----------------------|-------------|
| 4                     | 6           |
| 5                     | 10          |
| 6                     | 13          |
| 7                     | 12          |
| 8                     | 8           |
| 9                     | 4           |
| 10                    | 6           |
| 11                    | 9           |
| 12                    | 8           |
| 13                    | 152         |
| Total                 | 228         |

**FIG. 2.** Comparison of total body length measurements made directly from specimen (i.e. from point 1 to point 57 in Fig. 1B) with that summed across individual sclerite lengths measured as described in the text (see also Fig. 1A). Comparison is based only on articulated specimens (n = 170) because total body length cannot be measured directly from partially disarticulated specimens. Grey line indicates 1:1 line.

**FIG. 3.** Natural log (ln) of body length (measured in mm) for all *Elrathia kingii* specimens, arranged by number of thoracic tergites (n = 228).
length of the cephalon at the earliest meraspid stage was 0.55 mm. Even though the posterior part of the trunk grows at the fastest rates, the meraspid pygidium maintained an average length of 0.47 mm throughout ontogeny (Fig. 6) because a new thoracic tergite was released from the anterior section of the pygidium at each stage.

There was a 33% increase in growth rates across the gradient along the trunk during meraspis (Fig. 7). This decreased to 6% during holaspis, accompanied by a strong decrease in maximum growth rates along the gradient (Fig. 7). The growth gradient was much shallower during the holaspid period than during the meraspid period.

The meraspid growth gradient for *Elrathia kingii* is similar in concavity ($\lambda$) to that for *Aulacopleura koninckii*, but minimum and maximum ($a, a+b$) rates are higher in *E. kingii* (Fig. 7). The holaspid growth gradient is shallower in *E. kingii*, indicating that growth along the trunk was closer to constant in this species, compared with *A. koninckii*, but as with the meraspis gradient, minimum and maximum ($a, a+b$) rates are higher. Similarly, the cephalic growth rate is also higher in *E. kingii* than it is in *A. koninckii* (Table 2). In contrast, estimated cephalic and pygidial lengths at the start of the meraspis period are smaller in *E. kingii* compared with *A. koninckii*, and the terminal number of thoracic tergites and estimated total number of moults is smaller (Table 2).

Shape change in the cranidium of *Elrathia kingii* early in ontogeny is strongly allometric, but the rate of shape change decreases later in ontogeny (Fig. 8A). Overall shape change is best characterized by a threshold model with a break at ln centroid size 1.6 (Table 3). Ln centroid size of the cranidium in specimens with 12 thoracic tergites ranges from 1.50 to 1.61, and the minimum ln centroid size of the cranidium for specimens with 13 thoracic tergites is 1.58 (Fig. 8B), indicating that the change in allometry coincides with the transition from meraspis/anamorphosis to holaspis/epimorphosis.

**DISCUSSION**

The rate of cranidial shape change decreased at the transition from meraspis/anamorphosis to holaspis/epimorphosis in *Elrathia kingii*. A shift in the rate of shape change in the cranidium has been documented for other trilobites as well, and shown to be usually (but not always) coincident with transition into the holaspis period (Hopkins & Pearson 2016). In contrast, the pygidium in

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**FIG. 4.** Natural log (ln) of cephalic length (measured in mm) for all *Elrathia kingii* specimens, arranged by number of thoracic tergites ($n = 228$).

**FIG. 5.** Schematic diagram showing use of OLS regression (thick solid grey line) to assign holaspis specimens to moult stages based on cephalic length, rounding to the nearest integer. Dashed grey line is extrapolation of regression line; white dashed line shows the estimated moult stages for two specimens with different sized cephalae (20 and 25 moults, respectively). Based on this approach, the maximum body length was achieved over 28 moults.
E. kingii became more morphologically distinct from the thorax during holaspis (see Systematic Palaeontology). Presumably this is because the pygidium was no longer releasing the anteriormost segment into the thorax, so there was less functional constraint on its morphology. A practical outcome of this is that it is much easier to distinguish between the thorax and the pygidium in large specimens (see Systematic Palaeontology).

Both Elrathia kingii and Aulacopleura koninckii show a shift to a lower, shallower growth gradient across the trunk in the holaspis period (Fig. 7). However, growth rates are higher in E. kingii, both across the trunk as well as for the cephalon (Table 2). Aulacopleura koninckii starts growth in the meraspid period at a larger size and adds more thoracic tergites to the body during meraspis (Table 2), which also means that A. koninckii individuals spent a greater proportion of their lifespans growing under a stronger growth gradient than E. kingii individuals (58–68% compared with 43% of the total estimated number of post-protaspis mouls). Thus at the earliest point at which A. koninckii transitions to the holaspis period (number of thoracic tergites = 17), total body length is larger than at the same life history transition in E. kingii. Ultimately, however, E. kingii exceeds A. koninckii in maximum body length by maintaining higher growth rates across all life history stages and sclerites over a similar number of total moult stages. In short, higher growth rates in E. kingii compensate for smaller body lengths at M0 and fewer thoracic tergites in achieving similar body lengths to A. koninckii.

The larger average total length of M0 estimated for Aulacopleura koninckii compared with Elrathia kingii (1.220 mm and 1.027 mm, respectively) implies that the latest-stage protaspids in the former species were also larger, and if growth rates were constant within the protaspis phase, that A. koninckii also had larger earliest-stage protaspids. Variation in earliest-stage protaspids is certainly possible, especially of the magnitude implied here by the different estimates of body length at M0. For example, Laibl et al. (2014) described three stages of morphologically similar protaspids from each of two co-occurring species, Sao hirsuta and Ptychopariida sp. A’ for which the size of each protaspid stage varied (e.g. the

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**FIG. 6.** Natural log (ln) of pygidial length (measured in mm) for all Elrathia kingii specimens, arranged by number of thoracic tergites (n = 228).

**FIG. 7.** Growth gradients for the meraspid and holaspis periods of Elrathia kingii and Aulacopleura koninckii. Gradients were estimated by fitting an exponential decay curve to per-tergite growth rates vs relative position of the tergite at that growth stage. See text for more details.
For purposes of comparison, the average body length for holaspid could have occurred at a larger range of body length. A. konincki had a variable number of terminal segments, the transition to the holaspid stage. Because A. konincki represented the meraspid period, and represents the minimum body length at the transition to the holaspid stage.

Parameters are compared with those estimated from Aulacopleura konincki using data from Hughes et al. (2017; see also Hopkins 2020b). The average body length at the meraspid–holaspid transition was estimated as the average length of specimens with 12 thoracic tergites in Elrathia kingii, which is the penultimate number of thoracic tergites. Because A. konincki had a variable number of terminal segments, the transition to holaspid could have occurred at a larger range of body length. For purposes of comparison, the average body length for A. konincki was measured for specimens with 17 thoracic tergites, which is the largest number of thoracic tergites guaranteed to represent the meraspid period, and represents the minimum body length at the transition to the holaspid stage.

Length of P1 in Sao hirsuta ranged from 0.62 to 0.71 mm, whereas the length of P1 in 'Ptychopariida sp. A' ranged from 0.51 to 0.61 mm). Further, there is greater variation in egg and larval size across living arthropods, even between closely related species (e.g. eggs of Gulf of Mexico fiddler crab species vary from 0.25 ± 0.2 mm to 1.0 ± 0.1 mm; Thurman 1985).

Elrathia kingii and Aulacopleura konincki differ in some aspects of morphology, such as the terminal number of segments, but overall they are largely similar in dorsal exoskeletal morphology. For example, both show narrow (sag.) axial lobes and wide (tr.), narrow (sag.) pleural regions of the tergites, consistent with the 'olenimorph' body type (Fortey & Owens 1997). With this in mind, it may be unsurprising that they are so similar in growth parameters, even despite their vast difference in geological age (Cambrian for E. kingii and Silurian for A. konincki).

However, these datasets are the only two of their kind. This puts a fine point on the need for further empirical studies, given the large diversity of exoskeletal morphology, body size, and body proportions in trilobites.

**TABLE 2.** Growth rate estimates and other size parameters estimated for Elrathia kingii.

| Parameter | E. kingii | A. konincki |
|-----------|-----------|-------------|
| Cephalic per-moult growth rate | 1.121 | 1.085 |
| a (meraspid) | 1.094 | 1.059 |
| a (holaspid) | 1.109 | 1.084 |
| a + b (meraspid) | 1.445 | 1.370 |
| a + b (holaspid) | 1.172 | 1.168 |
| Estimated cephalon size at M0 (mm) | 0.554 | 0.671 |
| Estimated pygidium size at M0 (mm) | 0.473 | 0.549 |
| Max. no. moults | 28 | 31 |
| Terminal no. thoracic tergites | 13 | 18–22 |
| Maximum total body size (mm) | 36.80 | 29.25 |
| Average body size at meraspid-holaspid transition (mm) | 4.89 | 7.22 |

Parameters are compared with those estimated from Aulacopleura konincki using data from Hughes et al. (2017; see also Hopkins 2020b). The average body length at the meraspid–holaspid transition was estimated as the average length of specimens with 12 thoracic tergites in Elrathia kingii, which is the penultimate number of thoracic tergites. Because A. konincki had a variable number of terminal segments, the transition to holaspid could have occurred at a larger range of body length. For purposes of comparison, the average body length for A. konincki was measured for specimens with 17 thoracic tergites, which is the largest number of thoracic tergites guaranteed to represent the meraspid period, and represents the minimum body length at the transition to the holaspid stage.

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**SYSTEMATIC PALAEONTOLOGY**

Class TRILOBITA Walch, 1771
Order AULACOPLEURIDA Adrain, 2011
Family ALOKISTOCARIDAE Resser, 1939

**Genus ELRATHIA Walcott, 1924**

Type species. Conocoryphe (Conocephalites) kingii Meek, 1870; from the Cambrian of Utah, USA.

**Elrathia kingii** (Meek, 1870)

Figures 9–11, 12A, B, E, F, I, J, M, N, R, S, 13

1870 Conocoryphe (Conocephalites) kingii Meek, pp. 63–64.
1877 Conocoryphe (Ptychoparia) kingii; Meek, p. 20, pl. 1, fig. 4.
1886 Ptychoparia kingii; Walcott, p. 193, pl. 27, figs 4, 4a.
1924 Elrathia kingii; Walcott, p. 56, pl. 11, fig. 4.
1925 Elrathia kingii; Walcott, p. 87, pl. 15, figs 1–4.
1944 Elrathia kingii; Shimer & Shrock, p. 611, pl. 255, figs 5, 6.
1954 Elrathia kingii; Palmer, p. 78, pl. 17, fig. 13.
1959 Elrathia kingii; Bright, pp. 83–88, pl. 17, 18.
1964 Elrathia kingii; Robison, p. 542, pl. 85, figs 1–5, 21.
1981 Elrathia kingii; Gunther & Gunther, p. 32, fig. 23, pl. 18.

Type specimen (syntype). Complete exoskeleton (USNM PAL 8577) from Antelope Springs, House Range, Utah.

**Material.** Over 450 specimens were examined from the Wheeler Formation, North Antelope, House Range, Millard County, Utah. Specimens are housed at the American Museum of Natural History under accession number 67221.

**Diagnosis.** Emended from Robison (1964): Species of Elrathia with relatively narrow axis. Anterior border horizontal or only slightly upturned. Palpebral lobes about one-half glabellar length. Terminal number of thoracic tergites is 13. Pygidium has four axial rings and a terminal piece that is sometimes subdivided by a faint ring furrow. Posterior margin of pygidium usually marked by broad medial notch. Dorsal surface has very fine (10–20 μm scale) granulation, most highly concentrated on the posterior half of the cephalon and anterior part of the thorax; caeca present on the frontal area and librigenal (Fig. 9).
**Description.** See Meek (1870) and Palmer (1954) for detailed description of dorsal exoskeleton. The description is extended here to include ventral morphology and body size information.

Hypostome (Fig. 10A–C) lingulate, with gently curved, narrow anterior border, and strongly rounded narrow posterior border. Lateral margin widens at the shoulder, then curves laterally to meet acutely angled anterior wing. Pit of wing process strongly expressed. Middle body is longer (sag.) than wide (tr.), with posterior lobe slightly wider (tr.) than anterior lobe. Anterior lobe of middle body separated from posterior lobe by posteriorly directed middle furrow, which becomes more weakly expressed posteriorly. Rostral plate hemicylindrical (Fig. 10D, E, G), broadly curved at anterior margin (rostral suture). Body of plate 2.5-fold as wide (tr.) as long (sag.). Anterior and posterior wings long, narrow with lateral edges (connective sutures) strongly convex adaxially. Terrace lines on anterior ventral margin of rostral plate and on doublure of librigenal (Fig. 10D).

**FIG. 8.** Shape change in the cranidium during ontogeny of *Elrathia kingii*. A, amount of relative shape change, as described by the partial Procrustes distance between each specimen and the smallest specimen. B, natural log (ln) of centroid size of each cranidium plotted against the number of thoracic tergites in the trunk of the specimen associated with that cranidium. Vertical grey line is at ln centroid size 1.6, which is associated with both the transition to a lower rate of shape change in the cranidium (Table 3) and the transition to holaspis/epimorphosis.

**TABLE 3.** Results of model comparison for *Elrathia kingii*.

| Model type   | Break position (ln centroid size of cranidium) | AICc  | AICc weights |
|--------------|-----------------------------------------------|-------|--------------|
| Linear model | NA                                            | −708.9006 | 0.000        |
| Threshold model | 1.1                                            | −803.3794 | 0.000        |
| Threshold model | 1.2                                            | −824.1989 | 0.000        |
| Threshold model | 1.3                                            | −833.2647 | 0.011        |
| Threshold model | 1.4                                            | −835.5075 | 0.035        |
| Threshold model | 1.5                                            | −837.4314 | 0.092        |
| **Threshold model** | **1.6**                                        | **−841.2753** | **0.628**    |
| Threshold model | 1.7                                            | −838.8330 | 0.185        |
| Threshold model | 1.8                                            | −836.0679 | 0.047        |
| Threshold model | 1.9                                            | −828.3359 | 0.001        |
| Threshold model | 2.0                                            | −817.7730 | 0.000        |

Better support is indicated by lower Akaike information criterion corrected for small sample size (AICc). AICc weights indicate the relative likelihood of each model; these are normalized to sum to 1 and may be interpreted as probabilities. Best supported model is shown in bold.

**FIG. 9.** Ornamentation on holaspis specimens of *Elrathia kingii*. A, close-up of B showing very fine granulation on cephalon and thorax, and genal caeca on librigena. B, midsize holaspis, 13.7 mm in length, AMNH-FI-115708. C, smaller holaspis, 9.3 mm in length, AMNH-FI-115548. D, close up of C showing glabellar furrows, occipital node, and granulation on cephalon and thorax. E, close up of left anterior thoracic tergites (left box on G) showing very fine granulation on exoskeleton and faint fine pits on internal mould; this area was exposed after mechanical preparation of the specimen. F, close up of right anterior thoracic tergites, showing fainter fine granulation; this area was previously exposed to weathering. G, larger holaspis, 20.9 mm in length, AMNH-FI-115584; dashed line shows margin of area that was mechanically prepared. H, close up of librigenal showing strong expression of caeca on internal mould of frontal area and librigena, AMNH-FI-115669. Scale bars represent: 2 mm (B, C, G); 0.5 mm (A, D, E, F, H).
Transition to holaspid period occurs at c. 5 mm in total body length. In the examined collection, holaspids range from 4.9 to 36.8 mm in total body length.

**Occurrence.** Geological range: Wheeler and Marjum Formations, upper *Ehmaniella* and *Bolaspidella* Laurentian trilobite zones, upper Wuliuan – Drumian Stage, Miaolingian Series, Cambrian. Geographic range: House and Drum Ranges, Millard County, western Utah, USA.

** Ontogeny**

Accurate counting of the number of thoracic tergites in meraspis *Elrathia kingii* is challenging because the anteriormost segment in the meraspis pygidium resembles the posteriormost tergite in the trunk. The axial and the pleural furrows on the anteriormost segment are more strongly expressed than other furrows on the meraspis pygidium (Fig. 11), contributing to the impression that the anteriormost segment is an articulated sclerite rather than fused to the pygidium, especially when the lateral margin is not clearly defined against the matrix. Identifying the anterior margin of the pygidium is aided by the fact that at least three pygidial axial rings are visible on transitory pygidia (Fig. 11). The shape of the margin, differential expression of furrows, and minimum number of axial rings may be confirmed by comparison with isolated meraspis pygidia (Fig. 11).

There are several different types of protaspids as well as putative M0 specimens in the sampled material. As many as three protaspid instars have been described for *Bolaspidella housensis* (Lee & Chatterton 2005), which co-occurs in the collected samples, even occasionally on the same bedding surfaces. It is possible that more than one should also be assigned to *Elrathia kingii*, given that it is not uncommon for other trilobites in the Order Aulacopleurida to have three to four protaspid stages (Chatterton 1994; Chatterton & Speyer 1997; Chatterton et al. 1999; Hughes et al. 1999; Adrain 2011; Laibl et al. 2014). Given the similarities between *B. housensis* and *E. kingii* in early meraspis stages (see below), it has not yet been possible to confidently distinguish between *B. housensis* and *E. kingii* protaspids or M0-stage meraspids in the studied material. However, a complete meraspis sequence from M1 has been identified, forming the

**FIG. 10.** Ventral morphology of *Elrathia kingii*. A, isolated hypostome, 1.24 mm in length, AMNH-FI-134443. B, isolated hypostome, 0.96 mm in length, AMNH-FI-164176. C, isolated hypostome, 0.77 mm in length, AMNH-FI-134367. D, librigena articulated with rostral plate (in ventral view) and associated with hypostome, AMNH-FI-117226; cephalon was an estimated 2.8 mm long, a size associated with smaller holaspids (thoracic tergites = 13, see Fig. 4); the exposed part of the hypostome is 0.94 mm in length, possibly comparable to that shown in A. E, librigena (in dorsal view) associated with hypostome, AMNH-FI-134439; cranium was an estimated 6.3 mm long, a size associated with larger holaspids specimens; based on what is preserved, the hypostome is estimated to be 2.4 mm long, or twice as long as that shown in A. F, isolated hypostome, 1.34 mm in length, AMNH-FI-164462; note fine granulation on adjacent *E. kingii* cranium. G, isolated rostral plate showing terrace lines on anterior margin, AMNH-FI-164465. H, librigena, rostral plate, and hypostome shown of *Bolaspidella housensis*, AMNH-FI-164161; note that the hypostome is widest at the posterior margin, that the posterior lobe tapers, as well as the course granules on the associated librigenal, all of which distinguish this specimen from *E. kingii*. Scale bars represent: 0.5 mm (A–C, F–H); 2 mm (D, E).
basis for the following description of ontogeny in the dorsal exoskeleton.

**M1–M2.** Glabella twice as long (sag.) as wide (tr.); parallel-sided to slightly expanding anteriorly (Figs. 11, 12A, B, E, F). Preglabellar furrow coincident with straight anterior border furrow. Dorsal suture curves gently, expanding laterally towards posterior margin, with slight concavity at palpebral furrow. Palpebral lobes straight, posterior end at mid-length of glabella. Ocular field at and posterior to palpebral lobe wider than glabella. S0 straight. Posterior border of occipital ring gently concave posteriorly. Posterior border furrow straight laterally, curves posteriorly at width of posterior end of palpebral lobe. Posterior margin curves posteriorly at same point such that border widens to cover lateral end of anteriormost thoracic tergite. All furrows strongly expressed with exception of glabellar furrows S1–S4.

Axial rings of trunk consistent in length (sag.) but decrease in width (tr.) along the body to the terminal end of the rachis. Interpleural furrows straight laterally, curve posteriorly at fulcrum and end just before reaching the margin. Pleural fields of thoracic tergites narrow to a blunt point at posterior margin. Anteriormost interpleural furrow of pygidium slightly more strongly curved than interpleural furrow of posteriormost thoracic tergite. Pleural and interpleural furrows extend almost to margin of meraspid pygidium, curving more strongly posteriorly towards the posterior margin, interpleural furrows more strongly expressed than pleural furrows. Three to four axial rings visible in meraspid pygidium with narrow (tr.) terminal piece. Anteriormost axial ring of meraspid pygidium is often wider (tr.) than other axial rings; this plus the increased curvature of the interpleural furrows along the trunk can make it difficult to determine how many thoracic tergites there are. Meraspid pygidia often express the anteriormost segment as an emerging thoracic tergite about to be released (Fig. 11).

M1 meraspid of *Elrathia kingii* (Fig. 12A, B) are very similar in morphology to the co-occurring species *Bolaspidella housensis* (Fig. 12C, D). However, the latter has a more lenticular occipital ring than the oblong occipital ring of *E. kingii*, and the posterior limbs in *B. housensis* curve more strongly posteriorly, often obscuring the pleural field of the first thoracic tergite or the anterolateral margin of the pygidium pygidium. The anterior axial furrows on the cephalon tend to be more strongly expressed in *E. kingii* than in *B. housensis*. At the M2 and M3 stage, incipient nodes can be discerned on the occipital ring and axial rings in the meraspid pygidium of *B. housensis* (Fig. 12G, H, K, L); these are absent from *E. kingii* specimens (Fig. 12E, F, I, J). *Elrathia kingii* at the M4 stage and older (Figs. 12M, N, Q, R, 13) are easy to distinguish from the co-occurring species *B. housensis* because they lack axial spines whereas *B. housensis* has axial spines on the fourth to eighth thoracic tergites (Fig. 12O, P, S, T). *Bolaspidella housensis* is on average smaller than *Elrathia kingii* at all stages.

**M3.** Same as M1–M2 except that glabella is consistently parallel-sided (Fig. 12I, J). Dorsal suture is gently S-shaped with anterior dorsal suture convergent, and posterior dorsal suture straight and following the line of the palpebral furrow until curving posteriorly at posterior border. Palpebral lobe straight and parallel to anterior dorsal suture. Librigenal field narrow, oriented ventrally away from cranidium. Lateral margin curves smoothly to end of genal spine, which terminates at the anterior segment of meraspid pygidium.

**M4.** Same as M3 except that preglabellar furrow curves posteriorly away from anterior border furrow (Fig. 12M, N). Anterior border slightly bowed posteriorly at sagittal line to meet preglabellar furrow; curved posteriorly adaxially to meet the anterior border suture. Ocular field as wide (tr.) as glabella (tr.). Anterior and posterior margins curve smoothly to end of genal spine, which terminates at the third thoracic tergite. Cephalic spine smoothly curved, lateral furrow consistently expressed along librigena, terminates at posterior border furrow. 1.3–1.8 mm in total body length.

**M5.** Same as M4 except for short (sag.) preglabellar field and straight anterior border furrow at sagittal line. 1.8–2.3 mm in total body length (Fig. 12Q, R).

**M6.** Same as M5 except for relatively longer (sag.) preglabellar field (Figs. 11, 13A); anterior border suture less convergent forward, such that it curves forward relative to orientation of palpebral furrow; posterior dorsal suture curved laterally relative to palpebral furrow; and posterior border margin and furrow...
less strongly curved posteriorly. Pleural ends of thoracic tergites more strongly tapered to point. 2.2–2.5 mm in total body length.

**FIG. 13.** Later meraspid stages of *Elrathia kingii*. A, *E. kingii* with six thoracic tergites (M6), AMNH-FI-115593. B, *E. kingii* with seven thoracic tergites (M7), AMNH-FI-116846. C, *E. kingii* with eight thoracic tergites (M8), AMNH-FI-115557. D, *E. kingii* with nine thoracic tergites (M9), AMNH-FI-117184. E, *E. kingii* with 10 thoracic tergites (M10), AMNH-FI-115627. F, close up of E showing granulation on cephalon and thorax. G, *E. kingii* with 10 thoracic tergites and librigena (M10), AMNH-FI-115727. H, *E. kingii* with 11 thoracic tergites (M11), AMNH-FI-115638. I, *E. kingii* with 12 thoracic tergites (M12), AMNH-FI-115663; note also post-moult orientation of librigena. Scale bars represent: 0.5 mm (A–E); 1 mm (G–I).
away from palpebral lobe (Fig. 13B). Preglabellar furrow more gently curved. Straight, laterally oriented ocular ridge visible on some specimens. 2.5–2.9 mm in total body length.

M8. Same as M7, except anterior dorsal sutures slightly divergent before curving adaxially to meet anterior border (Fig. 13C). Preglabellar field as wide (sag.) as anterior border. S1 weakly expressed, does not meet axial furrow, oriented posteriorly and adaxially from lateral margin. 2.8–3.1 mm in total body length.

M9. Same as M8, except preglabellar field slightly longer (sag.) than anterior border, and posterior dorsal suture extends laterally before curving posteriorly to meet posterior border (Fig. 13D). Axial furrows slightly convergent towards gently rounded preglabellar field. Palpebral furrows parallel to axial furrows. 3.3–3.7 mm in total body length.

M10–12. Same as M9, except that relative length (sag.) of preglabellar field continues to increase, anterior dorsal suture continues to become more divergent. Anterior border increasingly straight laterally (Fig. 13E–I). S2 more strongly expressed, slightly curved towards sagittal axis. S3 weakly expressed, short, oriented similarly to S2, neither meets the axial furrow. M10: 3.8–4.1 mm in total body length; M11: 4.2–4.9 mm in total body length; M12: 4.6–5.4 mm in total body length.

Summary. From the M4 stage, the preglabellar field becomes relatively wider (sag.), the anterior dorsal suture transitions from being convergent forward to divergent forward before curving anteriorly to meet the anterior border, the glabella becomes more tapered, the palpebral furrow follows the axial furrow in orientation, the posterior dorsal suture extends laterally more strongly before curving posteriorly to meet the posterior margin, and the width (tr.) of the fixigenal field decreases relative to the width of the glabella. The pleural fields of the thoracic tergites increasingly taper more strongly towards blunt points. Throughout ontogeny, the genal spines consistently reach to the third thoracic tergite (or the comparable segment on the meraspis pygidium for M1–M3). Cephalic morphology stabilizes at the transition from M12 to holaspid (Figs 8, 9, 13G, H).

The hypostome moves progressively posteriorly, in conjunction with the expansion of the preglabellar field. The smallest hypostoma recovered are more droplet-shaped than lingulate, with a straight anterior margin and wide posterior border (Fig. 10C). During ontogeny, the posterior lobe of the middle becomes less wide relative to the anterior body (compare Fig. 10A–C).

Although the shape of the cranidium changes very little during holaspid (Figs 8, 9), the separation of the posteriormost thoracic tergite from the pygidium becomes more apparent with increasing size. In addition, the lateral part of the pygidial marginal border broadens (the pleural and interpleural furrows do not reach as far) and becomes more oblique relative to the rest of the pleural field. The posteriormost part of the marginal border becomes narrower as the marginal indent becomes more strongly expressed, so that the terminal piece almost reaches the marginal border in the largest specimens (Fig. 9G).

Remarks

The original description of *Eratia kingii* (Meek 1870) was considerably detailed but included no separate diagnosis per se. Meek (1877) repeated the original description, with some additional notes regarding preservation of the specimens and taxonomic affinity. Likewise, Walcott (1886) repeated the original description verbatim, with an additional note regarding some taphonomic distortion of the type specimen. Palmer (1954) also repeated the original description verbatim but included a concise summary of pertinent identifying features in his discussion, focusing on the relatively narrow border on the cranidium and pygidium, short genal spines, and short distal thoracic spines. Robison (1964) was the first to explicitly provide a diagnosis.

Robison’s diagnosis included mention of ‘occasionally incipient anterolateral spines’ on the pygidium (p. 542). None of the specimens examined herein has visible incipient anterolateral spines. It is possible that *E. kingii* shows geographic or stratigraphic variation in this trait, or that these spines are more readily visible on some of the silicified material that Robison (1964) examined but did not figure (Robison 1964, pl. 85, figs 5, 21; compare with specimens of *Eratia marjumii* Robison, 1964, pl. 85, figs 10, 13 for which incipient spines are visible). Because of the apparent rarity of this trait on *E. kingii* as well as the lack of documentation of this trait in the literature, incipient pygidial anterolateral spines have been excluded from the emended diagnosis herein.

In his diagnosis, Robison (1964) also stated that the exoskeleton was smooth despite acknowledging that Bright (1959) noted granulation on a minority (5%) of specimens. In the examined collection, granulation is usually visible on meraspids (Fig. 13) and small holaspids (Figs 9C–D, 10F), while larger holaspid specimens are likely to appear smooth or with granulation confined to furrows (Fig. 9A, B). Granulation is very fine (increasingly so on large specimens), visible only after whitening of the specimen, and probably susceptible to weathering (Fig. 9E, F; see also Hopkins 2019), which may contribute to the impression that it is often confined to furrows on large specimens. Bright (1959) did not mention whitening specimens, so it is possible that his reported percentage of specimens with granulation is a severe underestimate. The exoskeletal material of *E. kingii* specimens from the Wheeler Formation is also recrystallized (Bright 1959; Gaines & Droser 2003), and it is possible that granulation on some specimens was lost during calcite replacement, or differentially preserved at different localities. Nonetheless, where visible, granulation is concentrated on the cephalon and thorax with low to no concentration on the pygidium; this is consistent with Bright (1959)’s observations. Faint caeca on the cephalon were noted in the original description by Meek (1870). In the examined collection, caeca are frequently visible (particularly after whitening) on the frontal area of the cranidium and genal area of the librigena on holaspids (Fig. 9A), but rarely on meraspids (Fig. 13); it is also more strongly expressed on the internal mould (Fig. 9H). The diagnosis has been emended to reflect these observations. Furrows are also differentially expressed in different preservational modes. For example, the pygidial axial
ring furrows may be more distinct on silicified material (Robison 1964) than on the specimens preserved with cone-in-cone calcite incrustations. Often only three axial rings are well-defined, with the fourth indicated by shallow furrows on the middle part of the rachis or as indents along the axial furrow. It is particularly difficult to see more than three rings on meraspid specimens where the rachis may be only a few hundred microns in length and the terminal piece is relatively small. Although four axial rings are almost always visible on larger specimens (greater than 20 mm in body length; 3 mm in pygidial length), specimens where four rings are visible comprise the entire size range (in length) of holaspids. A conservative interpretation of this variation is that the transition from anamorphosis to epimorphosis is coincident with the transition from meraspid to holaspid stages (i.e. *Elrathia kingii* is synarthromeric), and that the expression of the fourth pygidial axis is sensitive to preservation and is more easily (but not exclusively) seen on larger specimens. It may be possible to independently verify this interpretation through renewed study of disarticulated silicified material, where the expression of furrows is sometimes more clearly preserved, while making use of the size information for different moults provided herein.

Meek (1870) described the glabella as having ‘lateral furrows not clearly defined…but apparently consisting of four pairs’ (p. 63). In the examined collection, two pairs of glabellar furrows (interpreted as S2 and S3) are sometimes visible as obliquely oriented shallow furrows that do not reach the axial furrows or across the sagittal axis; the posterior pair is usually twice as long as the anterior pair (Figs 9C, D, 13F, G). An occipital node is also present, becoming increasingly small with size (Figs 9D, G, 13), but this trait is not unique to *E. kingii* among congeners (e.g. *Elrathia groenlandica* Geyer & Peel, 2017, fig. 11; *Elrathia marjumi* Robison, 1964, pl. 85, fig. 8).

The ventral morphology of the librigena for *Elrathia kingii* was figured and described by Robison (1964) based on silicified material from the Wheeler Formation of the Wheeler Amphitheatre (House Range, Utah), along with rostral plates for congeneric species. This paper is the first, however, to include a description and imaging of the hypostome for any *Elrathia* species, as well as the rostral plate for *Elrathia kingii*. The rostral plate in *E. kingii* is narrower (tr.) than those for *E. marjumi* and *E. alapyge* Robison, 1964 (compare Fig. 10D with Robison 1964, pl. 85, figs 6, 14).

The position and relative size of the hypostome was previously known from indentations associated with fracturing of the glabella (e.g. USNM PAL 15439d, in Palmer 1954, pl. 17, fig. 13), which indicated that the anterior margin of the hypostome was coincident with the preglabellar furrow in holaspid specimens. Because the length of the preglabellar field increased during the latter part of the meraspid phase, the hypostome would have become progressively further removed from the anterior border during ontogeny. However, for all stages with four or fewer thoracic tergites, the preglabellar furrow was coincident with the anterior border furrow, which itself is positionally coincident with the posterior margin of the rostral plate on the ventral side. Geometrically speaking, the hypostome could have been attached to the rostral plate in these early stages. *Elrathia* hypostoma at all ontogenetic stages are distinguishable from *Bolaspidella* hypostoma by the overall proportions, and the expression of the furrows. Specifically, the hypostome in *Elrathia* is widest at the anterior wings and the middle furrows gently curve abaxially, whereas the hypostome in *Bolaspidella* is widest at the anterior margin and the middle furrows are directed obliquely so that the anterior body tapers posteriorly (Fig. 10H).

Bright (1959, p. 88, pl. 17) figured two specimens with fewer than 13 tergites, which he referred to as meraspids. He also reported a small proportion of putative holaspid specimens with fewer than 13 tergites: specifically of 400 specimens, eight were reported to have 12 tergites, one to have 11 tergites, and one to have 10 tergites. There was no indication why these were considered holaspids as opposed to meraspids. The smallest specimen that he measured was c. 5 mm in total length, which is just larger than the mean body length of meraspid specimens with 12 tergites examined for this study. There is some overlap in body length of the largest meraspids and smallest holaspids in the examined collection (Fig. 3), but there are no specimens greater than 5.3 mm with fewer than 13 tergites. It is thus possible that the ‘holaspids’ with aberrant tergite counts were actually large meraspids. Unfortunately, the whereabouts of the collection that Bright studied is unknown, so it is not possible to confirm or reject this conjecture. Until larger specimens with fewer than 13 tergites are documented, *Elrathia kingii* should be considered to have an invariant terminal number of thoracic tergites.

*Elrathia kingii* is the type species of the genus. Robison (1964) referred to *Elrathia* as a ‘wastebasket genus’ and restricted the genus to *E. kingii*, *E. alapyge*, *E. marjumi*, *Elrathia alabamensis* Resser, 1938, and *Elrathia georgiensis* Resser, 1938, while acknowledging that as many as 10 putative species could not be definitively included or excluded based on available material. Geyer & Peel (2017) provided comparative descriptions of congeneric species described from North America since 1964, with the exception of *Elrathia antiquata* Schwimmer, 1989, which had been designated the senior synonym for *E. alabamensis* and *E. georgiensis* (Schwimmer 1989). Only *E. kingii* has been reported from the Wheeler Formation, but all three Utahan species (*E. kingii*, *E. alapyge*, and *E. marjumi*) have been reported from the Marjum Formation (Robison 1964; Robison et al. 2015; Foster & Gaines 2016).

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REFERENCES

ADRAIN, J. M. 2011. Class Trilobita Walch, 1771. 104–109. In ZHANG, Z.-Q. (ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa, 3148.

BARRANDE, J. 1846. Notice préliminaire sur le Système Silurien et les Trilobites de Bohême. Hirschfeld, Leipzig, 96 pp.

BRIGHT, R. C. 1959. A paleoecologic and biometric study of the Middle Cambrian trilobite Elrathia kingii (Meek). Journal of Paleontology, 33, 83–98.

BURNHAM, K. P. and ANDERSON, D. R. 2002. Model selection and multimodel inference, 2nd edition. Springer, 488 pp.

CHATTERTON, B. D. E. 1994. Ordovician proetid trilobite Dimeropyge, with a new species from northwestern Canada. Journal of Paleontology, 68, 541–556.

——— and SPEYER, S. E. 1997. Ontogeny. 173–247. In KAESLER, R. L. (ed.) Treatise on invertebrate paleontology. Part O. Arthropoda 1. Trilobita (Revised). Geological Society of America & University of Kansas Press.

——— EDGECOMBE, G. D., VACCARI, N. E. and WAISFELD, B. G. 1999. Ontogenies of some Ordovician Telephinidae from Argentina, and larval patterns in the Protida (Trilobita). Journal of Paleontology, 73, 219–239.

DRYDEN, I. 2018. shapes package. v. 1.2.4. http://cran.r-project.org/web/packages/shapes/index.html

FORTEY, R. A. and OWENS, R. M. 1997. Evolutionary history, 249–287. In KAESLER, R. L. (ed.) Treatise on invertebrate paleontology. Part O. Arthropoda 1. Trilobita (Revised). Geological Society of America & University of Kansas Press.

Foster, J. R. and Gaines, R. R. 2016. Taphonomy and paleontology. 249–287. In Foster, J. R. and Gaines, R. R. (eds). Arthropod biology and evolution: Molecules, development, morphology. Springer.

——— Hughes, N. C., Webster, M. and MINELLI, A. 2004. Exploring developmental modes in a fossil arthropod: growth and trunk segmentation of the trilobite Aulacopleura konincki. American Naturalist, 163, 167–183.

——— Garland, J. T., Hunt, G. and Hughes, N. C. 2012. Developmental trait evolution in trilobites. Evolution, 66, 314–329.

——— Hong, P. S. and Hughes, N. C. 2014. Positional specification in the segmental growth pattern of an early arthropod. Proceedings of the Royal Society B, 281, 20133037.

——— ———— 2016. Axial growth gradients across the postproaspid ontogeny of the Silurian trilobite Aulacopleura konincki. Paleobiology, 42, 426–438.

Gaines, R. R. and DROSER, M. L. 2003. Paleocology of the familiar trilobite Elrathia kingii: an early exaerobic zone inhabitant. Geology, 31, 941–944.

Geyer, G. and Peel, J. S. 2017. Middle Cambrian trilobites from the Ekspedition Bræ Formation of North Greenland, with a reappraisal of the genus Elrathia. Journal of Paleontology, 91, 265–293.

Gunther, L. F. and Gunther, V. G. 1981. Some Middle Cambrian fossils in Utah. Brigham Young University Geology Studies, 28, 87.

Haber, A. 2015. The evolution of morphological integration in the ruminant skull. Evolutionary Biology, 42, 99–114.

Hopkins, M. J. 2017. Development, trait evolution, and the evolution of development in trilobites. Integrative & Comparative Biology, 57, 488–498.

——— 2019. Phylogenetic analysis and revision of the trilobite subfamily Baltimarginatinae (Olenidae). American Museum Novitates, 3928, 1–20.

——— 2020a. Data from: Ontogeny of the trilobite Elrathia kingii (Meek), and comparison of growth rates between Elrathia kingii and Aulacopleura konincki (Barrande). Dryad Digital Repository. https://doi.org/10.5061/dryad.47d7wm39n

——— 2020b. A simple generative model of trilobite segmentation and growth. Paleo Rx iv, 27 January. https://doi.org/10.31233/osf.io/zt642

——— and Pearson, J. K. 2016. Non-linear ontogenetic shape change in Cryptolithus tesselatus (Trilobita) using three-dimensional geometric morphometrics. Palaeontologia Electronica, 19.3.42A, 1–54.

——— Haber, A. and Thurman, C. L. 2016. Constraints on geographic variation in fiddler crabs (Ocypodidae: Uca) from the western Atlantic. Journal of Evolutionary Biology, 29, 1553–1568.

Hughes, N. C., Chapman, R. E. and Adrain, J. M. 1999. The stability of thoracic segmentation in trilobites: a case study in developmental and ecological constraints. Evolution & Development, 1(1), 24–35.

——— Minelli, A. and Fusco, G. 2006. The ontogeny of trilobite segmentation: a comparative approach. Paleobiology, 32, 602–627.

——— Hong, P. S., Hou, J. and Fusco, G. 2017. The development of the Silurian trilobite Aulacopleura konincki reconstructed by applying inferred growth and segmentation dynamics: a case study in paleo-evo-devo. Frontiers in Ecology & Evolution, 5, 00037.

Klingenberg, C. P., Barluenga, M. and Meyer, A. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. Evolution, 56, 1909–1920.

Laibl, L., Fatka, O., Crónier, C. and Budil, P. 2014. Early ontogeny of the Cambrian trilobite Sao hirsuta from the Skryje-Týřovice Basin, Barrandian area, Czech Republic. Bulletin of Geosciences, 89(2), 293–309.

Lee, D.-C. and Chatterton, B. D. 2005. Protaspid ontogeny of Bolaspisella housensis (Order Ptychopariida, Class...
Trilobita), and other similar Cambrian protaspides. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 96, 21–41.

MEEK, F. B. 1870. Descriptions of fossils collected by the U.S. Geological Survey under the charge of Clerence King, Esq. *Proceedings of the Academy of the Natural Sciences of Philadelphia*, 22, 56–64.

——— 1873. Preliminary paleontology report, consisting of lists and descriptions of fossils, with remarks on the age of the rocks in which they are found. *Annual Report of the US Geological Survey of Territories*, 6, 429–518.

——— 1877. Paleontology. 1–197. In *Report of the Geological Exploration of the Fortieth Parallel Report, Volume IV, Part I*, Professional Papers of the Engineer Department, US Army.

MINELLI, A. and FUSCO, G. 2013. Arthropod post-embryonic development. 91–136. In MINELLI, A., BOXSHALL, G. and FUSCO, G. (eds). *Arthropod biology and evolution: Molecules, development, morphology*. Springer.

——— and HUGHES N. C. 2003. Tagmata and segment specification in trilobites. *Special Papers in Palaeontology*, 70, 31–43.

MOCZEK, A. P., SEARS, K. E., STOLLEWERK, A., WITTKOPP, P. J., DIGGLE, P., DWORKIN, I., LEDON-RETTIG, C., MATUS, D. Q., ROTH, S., ABOUHEIF, E., BROWN, F. D., CHIU, C.-H., COHEN, C. S., TOMASO, A. W. D., GILBERT, S. F., HALL, B., LOVE, A. C., LYONS, D. C., SANGER, T. J., SMITH, J., SPECHT, C., VALLEJO-MARIN, M. and EXTAVOUR, C. G. 2015. The significance and scope of evolutionary developmental biology: a vision for the 21st century. *Evolution & Development*, 17, 198–219.

PALMER, A. R. 1954. An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. *US Geological Survey Professional Paper*, 264-D, 55–86.

PARK, T.-Y. and CHOI, D. K. 2011. Constraints on using ontogenetic data for trilobite phylogeny. *Lethaia*, 44, 250–254.

R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

RASBAND, W. S. 2018. *ImageJ 1.47v*. http://rsb.info.nih.gov/ij/

RESSER, C. E. 1938. *Cambrian System (restricted) of the southern Appalachians*. Geological Society of America Special Papers, 15.

——— 1939. The *Ptarmigania* strata of the northern Wasatch Mountains. *Smithsonian Miscellaneous Collections*, 98(24), 1–72.

ROBISON, R. A. 1964. Late Middle Cambrian faunas from western Utah. *Journal of Paleontology*, 38, 510–566.

——— BABCOCK, L. E. and GUNther, V. G. 2015. Exceptional Cambrian fossils from Utah: A window into the age of trilobites. *Miscellaneous Publication*, 15-1. Utah Geological Survey, 97 pp.

SCHWIMMER, D. R. 1989. Taxonomy and biostratigraphic significance of some Middle Cambrian trilobites from the Conasauga Formation in western Georgia. *Journal of Paleontology*, 63, 484–494.

SHIMER, H. W. and SHROCK, R. R. 1944. *Index fossils of North America*. John Wiley & Sons, 837 pp.

THURMAN, C. L. 1985. Reproductive biology and population structure of the fiddler crab *Uca subcylindrica* (Stimpson). *Biological Bulletin*, 169, 215–229.

URDY, S., WILSON, L. A. B., HAUG, J. T. and SANCHEZ-VILLAGRA, M. R. 2013. On the unique perspective of paleontology in the study of developmental evolution and biases. *Biological Theory*, 8, 293–311.

WALCH, J. E. I. 1771. *Die Naturgeschichte der Versteinerungen, Dritter Theil*. Paul Jonathan Felstecker, Nuremberg, 235 pp.

WALCOTT, C. D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *Bulletin of the United States Geological Survey*, 30, 369 pp.

——— 1924. Cambrian Geology and Paleontology V. No. 2, Cambrian and Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, 75, 53–60.

——— 1925. Cambrian Geology and Paleontology V. No. 3, Cambrian and Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, 75, 64–144.