Modularity in the trilobite head consistent with the hypothesized segmental origin of the eyes

Ernesto E. Vargas-Parra | Melanie J. Hopkins

Division of Paleontology, American Museum of Natural History, New York, New York, USA

Correspondence
Ernesto E. Vargas-Parra, American Museum of Natural History, Central Park West at 79th St, New York, NY 10024, USA.
Email: evargas-parra@amnh.org

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Abstract
The trilobite head served multiple functions and was composed of several fused segments. Yet, the underlying organization of the trilobite head, and whether patterns are conserved across trilobites, remains unclear. Modeling the head as being composed of modules, or subunits that vary and thus have the potential to evolve semi-independently can reveal underlying patterns of organization. Hypotheses of modular organization based on the comparative developmental biology of arthropods were evaluated using geometric morphometrics. Two-dimensional (semi)landmark datasets collected from the cranidia of two Ordovician trilobite species, *Calyptaulax annulata* (Phacopida) and *Cloacaspis senilis* (Olenida sensu Adrian, 2011) were analyzed. The degree and pattern of modularity were assessed using the covariance ratio (CR), which compares the covariation within putative modules to the covariation between them, and the fit of different models was compared using an effect size measure derived from the CR. When treating the eyes as a distinct module, the best modular hypothesis identified for *C. annulata* shows the eyes and anteriormost region of the head integrated as a single module. The best modular hypotheses for *C. senilis* are more complex but the eyes still covary mostly strongly with the anterior part of the head. The latter is also the case for all other well-supported models for both species. These results can be interpreted as a developmental signal corresponding to the anteriormost ocular segment of early arthropods that is retained throughout development, despite any likely selective pressures related to functional needs.

KEYWORDS
modularity, integration, trilobite, ordovician, morphometrics

1 | INTRODUCTION

Trilobites are an extinct clade of crown-group arthropods (Daley et al., 2018). The underlying organization of the trilobite head is all but unknown. The trilobite head is a complex structure composed of several fused segments (Beecher, 1895; Henriksen, 1926; Palmer, 1957; Raw, 1957; Størmer, 1942; Hupé, 1959; Bergström, 1973a, 1973b; Park & Kihm, 2017) which served multiple functions including vision, feeding, digestion, and molting (Whittington et al., 1997). Relationships between different subregions of the head may be influenced by
functional and/or developmental coupling (Olson & Miller, 1958). For example, regions that coordinate to serve a common function are dependent on each other such that morphological change in one region is constrained by the other (Wagner & Schwenk, 2000). Likewise, regions corresponding to the same body segment share a developmental basis for where morphological change occurs in a coordinated fashion (Cheverud, 1996). The extent to which function and development shaped the trilobite head is not known but in either case, strong patterns of covariation would be expected. Identifying covariation patterns within and between regions of the head would elucidate its underlying organization and allow identification of functional or developmental drivers of this structuring.

Static modularity can provide a framework to study the underlying organization of the trilobite head. By focusing on (co)variation within multiple individuals of a single species at a particular ontogenetic stage (morphologically mature specimens, for instance), processes responsible for patterns of covariation within a homogenous, static sample can be determined (Klingenberg, 2014). Modeling the trilobite head as being composed of modules, or subunits that evolve semi-independently can reveal the organization of the trilobite head by assessing covariation between and within putative modules (Wagner & Altenberg, 1996; Wagner et al., 2007). The number and arrangement of modules are of interest here as they may indicate developmental or functional factors contributing to head organization (Goswami & Polly, 2010; Goswami, 2006).

The dorsal morphology of the trilobite head in most trilobites is composed of the cranidium, or medial sclerite, and two librigena which flank the cranidium and are separated by sutures that release during molting (Whittington et al., 1997). The cranidium is composed of the glabella, which is a medial lobe overlying part of the digestive system and often expresses furrows that have been interpreted to reflect the underlying musculature which, in turn, reflects segmentation of the head. Similarly, though rarely preserved, traces of the digestive system in some trilobites show a metameric organization of paired lateral lobes that correspond to glabellar furrows and thoracic segmental boundaries (Hopkins et al., 2017; Lerosey-Aubril et al., 2011; Ortega-Hernández & Brena, 2012). Most trilobites had large compound eyes on either side of the glabella. Although the eye lenses themselves are inconsistently preserved, they were typically overlain by a palpebral lobe at the lateral margins of the cranidium, which serves as a robust proxy for the size, shape, and position of the eyes on the head (Shaw, 1957).

Most of the trilobite fossil record is composed of disarticulated sclerites (Adrain & Westrop, 2016). Previously published studies on modularity in trilobites have focused on the cranidium because it is taxonomically useful, morphologically complex, and can be related to both development and function. For example, Webster and Zelditch (2011a) tested an a priori hypothesis of cranidial modularity related to functional association, but in finding little support for it, turned to an exploratory analysis in an effort to better understand how interactions among developmental pathways, as revealed by fluctuating asymmetry, influenced modular structure in the trilobite cranidium. Comparisons across closely-related species indicated that the modularity structure resulting from direct interactions can also be labile (Webster & Zelditch, 2011b). Gerber and Hopkins (2011) divided the cranidium into three modules describing the anterior part of the cranidium, the palpebral lobes, and the glabella and compared ontogenetic shape change at different local and global scales across a putative ancestor-descendent pair of species. If the cranidium was treated as a single unit, the ontogenetic trajectories of the cranidia for the two species diverged, consistent with allometric repatterning. However, the ontogenetic trajectories of individual modules overlapped with one another, consistent with heterochrony. In this case, the combination of local heterochronies led to a complex pattern of global allometric repatterning, indicating that morphological divergence can be achieved by differentially altering the timing of development along otherwise conserved trajectories. The Gerber and Hopkins (2011) study did not attempt to test the adequacy of their model relative to other possible models.

These previous studies conceptualized the modular structure of the trilobite head using knowledge of the segmented structure and functional significance of different parts of the cranidium. In this study, we test a hypothesis derived from comparative analysis across living arthropods: that the eyes are developmentally associated with the anterior part of the head, specifically that ocular structures are derived from tissues of the anterior most segment of the body, the “protocerebral segment,” even though the eyes may be spatially removed from the anterior region of the head in adults (Budd, 2002; Ortega-Hernández et al., 2017; Scholtz & Edgecombe, 2005, 2006). In the case of trilobites, the head is thought to be composed of five segments based on the expression of furrows and lobes of the glabella (Park & Kihm, 2017). In some trilobites, the eyes are connected to the anteriormost part of the glabella by eye ridges and are often associated with an S4 glabellar furrow (Bergström, 1973a, 1973b). This S4 furrow is argued to be incised within the first, anteriormost segment indicating an association between the eyes and
the ocular segment in trilobites. If signal of this early embryogenic origin of tissues is retained in the covariation structure of the morphologically mature adult trilobite, we expect to see patterns of modularity showing stronger association of the eyes with the anterior region of the head compared with the posterior region of the head.

2 | MATERIAL AND METHODS

2.1 | Material

To be able to divide the cranidium into regions associated with segmentation, two trilobite species with strongly expressed glabellar furrows were selected for analysis. Silicified specimens of *Calyptaulax annulata* (Raymond, 1905) were recovered from the Middle Ordovician Crown Point Formation, Valcour Island, New York (Shaw, 1968). Specimens used in this study were extracted from two stratigraphically adjacent horizons totaling 5 cm in thickness from an outcrop near Pebble Beach on the southern end of the island (believed to be the same locality as PB80-81 of Shaw, 1968). Rock samples were dissolved in buffered formic acid solution (Jeppsson & Anehus, 1995) and specimens were picked from sieved residues. The 37 cranidia of *C. annulata* analyzed in this study range from 1.45 to 4.08 mm in sagittal length.

Crack-out specimens of *Cloacaspis senilis* (Fortey, 1974) were collected from the Darriwillian (Middle Ordovician) Olenidsletta Member of the Valhallfonna Formation, Spitsbergen, Svalbard (Fortey, 1974; Kröger et al., 2017; Hopkins, 2019). Specimens used in this study were collected from a single horizon at a single locality (142 m in the PO section of Kröger et al., 2017). Specimens were mechanically prepared using a Swam Blaster® micro-abrasive blaster (Crystal Mark). The 34 cranidia of *C. senilis* analyzed in this study range from 2.50 and 11.94 mm in sagittal length. These sample sizes are comparable to that of other studies analyzing modularity in trilobites (Webster & Zelditch, 2011a, 2011b).

All specimens were whitened with ammonium chloride vapor and oriented for photography in dorsal view such that the palpebral lobes were horizontal, following Shaw (1957). The specimens were photographed using a Canon 60D SLR camera with either a Canon EF 100 mm f/2.8 Macro IS USM or MP-e65 mm f/2.8 1-5x Macro lens on a Stackshot macro rail system (Cognisys); composite images were produced using Zerene Stacker (Zerene Systems).

2.2 | Quantifying shape

Cranidial shape was quantified using geometric morphometrics. Two-dimensional landmarks and semilandmarks were collected using TPSDig2 (Rohlf, 2009). Twenty-eight landmarks and 110 semilandmarks (26 curves) were digitized from the cranidium of *C. annulata* (Figure 1a, Supporting Information: Table S1). Twenty-four landmarks and 84 semilandmarks (20 curves) were digitized from the cranidium of *C. senilis* (Figure 1b, Supporting Information: Table S2).

All subsequent analyses were performed in R 4.0.2 (R Core Team, 2021). Missing landmarks were estimated by reflecting corresponding paired landmarks across the midline and superimposed for object symmetry using the R functions AMP and OSymm, respectively (Haber, 2011a, 2011b; see Klingenberg et al., 2002 for discussion of object symmetry). Because these functions treat all landmarks as fixed, we then used the gpagen function from the R package geomorph 3.3.1 (Adams et al., 2021) to slide semilandmarks according to the Procrustes...
distance criterion (Zelditch et al., 2012). The resulting configurations comprise the symmetric component of the variation (Klingenberg et al., 2002). Having missing landmarks precluded us from assessing how much fluctuating asymmetric variation there was in the samples, but the symmetric component comprises the vast majority of variation in bilaterally symmetric shapes (see e.g., Webster & Zelditch, 2011a, 2011b). Shape variation explained by allometry was then removed by linear regression (allometry summarized 39.3% of shape variation in C. annulata and 6.1% of shape variation in C. senilis). Subsequent modularity analyses used the shape residuals from these regressions.

### 2.3 Modularity analysis

Generally treating the (semi)landmarks corresponding to the eyes as a single unit, multiple alternative hypotheses of modularity were constructed by partitioning cranial landmarks into segmental sections defined by glabella furrows. Differences in cranial morphology (such as in the expression of glabellar furrows and the shape of the anterior cranidium) between the two species warranted slightly different alternative modularity hypotheses. For C. annulata, 13 hypotheses of modularity were examined ranging from two-module models to a twelve-module model (Figure 2, Supporting Information: Figure S1). For C. senilis, 14 hypotheses of modularity were examined ranging from two-module models to a nine-module model (Figure 4, Supporting Information: Figure S3).

The covariance ratio (CR) was used to evaluate patterns of modular signal within modularity hypotheses because it is less sensitive to sample size and number of variables compared with other methods (Adams & Collyer, 2019; Adams, 2016). CR is a ratio of the covariation between modules relative to the covariation within them and is summed across all pairwise comparisons for models with more than two modules (Adams & Collyer, 2019; Adams, 2016). For a random set of variables, the CR value is expected to be 1. CR > 1 indicates that the covariation between modules is greater than the covariation within them. CR < 1 indicates greater covariation within modules than between them, which in turn is interpreted as a greater “degree” of modularity as the CR value gets smaller. The CR value for each modularity hypothesis was compared with a distribution of values obtained by randomly assigning landmarks into subsets (of the same number of landmarks in the original model); a small observed CR value relative to this distribution indicates significantly greater independence among modules than expected under the null hypothesis of random associations of variables (Adams, 2016). CR values and permutation tests were performed using the modularity.test function in the R package geomorph 3.3.1 (Adams et al., 2021).

Alternative modularity hypotheses were compared using an effect size measure ($Z_{CR}$) derived from the CR (Adams & Collyer, 2019). Models with the lowest $Z_{CR}$
values are considered the best fit to the covariation patterns in the sample, and significantly so if they fall outside empirically generated confidence intervals for competing models. Comparative tests of modularity were performed using the compare.CR function from the R package geomorph 3.3.1 (Adams et al., 2021).

2.4 Measurement error

To quantify measurement error from the placing of landmarks and semilandmark curves, the same image of a specimen of *C. annulata* was (semi)landmarked five times per day over the course of 7 days using the landmark scheme of the main analysis (Figure 1a) for a total of 35 configurations. This was done to achieve a comparable sample size to the main analysis. Data processing, superimposition, and modularity analyses were performed as described previously.

We found that the amount of variation attributable to measurement error is two orders of magnitude lower than the total variance in the data set in the main analysis (8.3 × 10\(^{-6}\) and 4.5 × 10\(^{-4}\), respectively, using the morphol.disparity function from the R package geomorph 3.3.1; Adams et al., 2021). The results of the modularity analysis (Supporting Information: Figure S6) show that the Z\(_{CR}\) values of the main analysis are overall more negative (better supported) than the Z\(_{CR}\) values of the measurement error analysis with no overlap in confidence intervals in all but one poorly supported modular hypothesis (M2c). Furthermore, in most modular hypotheses tested, Z\(_{CR}\) values of the main analysis are twice (or more) as negative as the values of the measurement error analysis.

3 RESULTS

For *C. annulata*, the best-supported model (M2d, CR = 0.6617, \(p = .001\)) has two modules, one comprising the eyes and the anteriormost part of the cranium (Figure 2), but the confidence interval encompasses the estimated Z\(_{CR}\) values for two other models: M2e (CR = 0.6768, \(p = .001\)) which differs in the assignment of the S3 glabellar furrow which defines the posterior part of the anterior lobe of the glabella (LA) and M5b (CR = 0.6071, \(p = .001\)) which differs in the division of the rest of the glabella into individual modules. Other more complex modular hypotheses (with a higher number of modules), such as M4a, M4b, and M5a are also relatively well supported, but in all cases, the eye module has the highest pairwise CR value (i.e., has the strongest association) with the module(s) corresponding to the anteriormost part of the cranium (Figure 3). This demonstrates higher covariation between these modules, relative to covariation within modules, compared with the other modules of the cranium. Interestingly, there are also higher CR values between the eyes and the anterior part of the glabella and lower CR values between either the eyes or the anterior part of the cranium and the posterior part of the glabella. This indicates a gradient of increasing modularity from the anterior to the posterior part of the glabella relative to both the anterior part of the cranium and the palpebral lobes (Figure 6a).

Two modular hypotheses (M4b, CR = 0.6249, \(p = .001\); M9a, CR = 0.5847, \(p = .001\)) were equally best supported by the covariation patterns in *C. senilis* (Figure 4). In the M4b model, the eyes and anterior margin comprise a module and the rest of the glabella is divided into additional partitions. In the M9a model, a comparison of pairwise CR values between partitions indicates that the eye most strongly covaries with the brim and anterior glabellar region (Figure 5c). The set of next-best supported models includes all the remaining with either four or more partitions (M4a, M4c, M5a, M5b, M6a). In all of these more complex models, the eye is most strongly integrated with the anterior margin of the cranium (see examples in Figure 5). As seen in *C. annulata*, there is also a gradient of lower CR values, indicating increasing modularity, from the anterior to posterior part of the glabella (Figure 6b).

3.1 Sensitivity of results to methodological choices

The trilobite cranidia analyzed in this study exhibit object symmetry (as opposed to matching symmetry, see Klingenberg et al., 2002). Such configurations have been represented by full configurations as well as a subset of landmarks comprising those along the line of symmetry and one-half of the paired landmarks on either side (Cardini, 2016; Zelditch et al., 2012). Previous studies assessing congruence between one-sided data and data based on both sides have shown that, while shape congruence may be high in analyses at a macroevolutionary level, congruence is much lower in an intra-specific sample (Cardini, 2016), and could influence the results presented here. In fact, using one-half of the configuration had a surprising impact on the relative Z\(_{CR}\) values of the best-supported models: in both species, the relative support for the models with two modules drops significantly while relative support for more complex models stayed the same (Supporting Information: Figure S2d, S4d). This might be related to the fact that
one-sided data exaggerates shape variation along the midline while reducing shape variation laterally off the midline (Bardua et al., 2019; Cardini, 2016). We attribute the smaller absolute values of the effect sizes to the decrease in the number of landmarks and removal of covariation across the sagittal axis.

Currently, two criteria are available for sliding semilandmarks during superimposition: the minimization of the bending energy or the minimization of the perpendicular distance to the curve referred to as the Procrustes distance criterion (Zelditch et al., 2012). Previous studies have demonstrated that these two methods for sliding semilandmarks can create large differences when morphological variation in a sample is small (Perez et al., 2006), as is the case here. In running the error analyses, we found that the bending energy approach results in an order of magnitude more variation in the superimposed landmarks than when using the Procrustes distance criterion ($2.8 \times 10^{-5}$ and $8.3 \times 10^{-6}$, respectively, using the morphol.disparity function from the R package geomorph 3.3.1; Adams et al., 2021). The difference in the landmark variation is also great enough to be seen visually by plotting the superimposed Procrustes coordinates on top of one another (Supporting Information: Figure S5, the point size for all configurations is exactly the same). As expected, when the Procrustes distance criterion is used, the semilandmarks vary along a line perpendicular to the curve. In contrast,
when the bending energy is used, the semilandmarks vary somewhat linearly and obliquely. This supports previous observations that the bending energy approach adds variation within the data (Sheets et al., 2006).

More troubling is the differential distribution of variation across the semilandmarks when the bending energy approach is used: semilandmarks that are along curves placed close together have more variation than those along more widely distributed curves (compare Supporting Information: Figure S5b to S5c). We interpret this to be the result of the more extreme curvature required of the bending energy plane when the curves are close together. We also suspect that the curves that are close together will have an elevated degree of covariation between them. This is borne out by comparison of two-module models where the anterior margin of the cranidium and the anterior margin of the glabella are either part of the same module (producing very low $Z_{CR}$ values, on the order of the results using the main data set) or not (producing very high $Z_{CR}$ values, on the order of the error analysis using Procrustes distance) (Supporting Information: Figure S7). Thus, the bending energy method may differentially introduce artificial covariation that can be of a magnitude much greater than measurement error and may be great enough to obscure the actual biological signal in the data. Further investigation of the pervasiveness of this across different landmark configurations is beyond the scope of this study but serves as a warning for anyone interested in using semilandmarks to investigate modularity patterns at low taxonomic scales.

Finally, $Z_{CR}$ values are similar whether or not allometry was accounted for in the sample for each species (Supporting Information: Figures S2b and S4b). This is expected as the sample consisted of morphologically mature specimens. Because allometry accounts for more variation in $C. annulata$ compared with $C. senilis$, $Z_{CR}$ values were affected more when removing allometry in the $C. annulata$ sample.

4 | DISCUSSION

The results of the modularity analyses for both trilobite species are consistent with each other. The best modularity models of the trilobite cranidium are those in which the eyes and anteriormost cranidium form a single module or, belong to two modules that highly covary relative to other modules. These models provided a significantly better fit to patterns of shape covariation compared with the many other hypotheses of modularity.
FIGURE 5 Pairwise CR values for partitions of the (a) M4b, (b) M5b, and (c) M9a modular hypotheses of the cranidium of *Calyptaulax senilis* with a diagram showing labeled partitions. M4b and M9a were the best-supported models. Of the set of next-best supported models (see Figure 4), M5b is representative of the distribution of pairwise CR values in that set. Higher pairwise CR values indicate greater covariation between modules. Circles are color-coded and sized according to pairwise CR values (warmer colors and larger sizes indicate higher pairwise CR values, respectively). Module labels correspond to upper-right diagrams in each panel.
tested. As mentioned in Section 1, structures in front of the glabella such as the pre-glabellar field and anterior glabellar border are considered outgrowths of the first segment (Park & Kihm, 2017). Thus, covariation patterns observed in the two trilobite species analyzed in this study, particularly between the eyes and anteriormost glabella, corroborate this proposed head segmentation of trilobites. Furthermore, these results can be interpreted as capturing a developmental signal pertaining to the ocular segment of early arthropods (Budd, 2002; Ortega-Hernández et al., 2017; Scholtz & Edgecombe, 2005, 2006). Although the trilobite head, like the head of all crown arthropods, is made up of fused segments, this developmental signal was retained in these two trilobites despite the ocular segment not being morphologically obvious. Interestingly, this purported developmental signal was not completely obscured or erased by other potentially overlapping developmental processes (as in the palimpsest model of Hallgrímsson et al., 2009). For example, dorsal closure of the head is observed during modern arthropod embryonic development (Chipman, 2015; Ortega-Hernández et al., 2017; Wolff & Hilbrant, 2011; Wolff, 2009). During this process, the ocular lobes may meet medio-dorsally and extend dorsally (Liu et al., 2009, 2010; McGregor et al., 2008; Ortega-Hernández et al., 2017; Posnien & Bucher, 2010), so much so that the ocular segment may potentially overlap immediately posterior head segments. Because trilobites are crown arthropods (Daley et al., 2018), it is likely that they also underwent this process during early development. If so, this may help to explain why glabellar furrows are more frequently obscured in the anterior part of the glabella compared with the posterior part (Hughes, 2003).

Although the covariation across the trilobite head is unlikely to have been unaffected by selective pressures, functional associations do not shape the pattern or degree of modularity in the trilobite head in an obvious way. For example, if function governed the underlying organization of the trilobite head one might expect structures such as the eyes (vision), glabella (digestion), and facial sutures (molting) to form exclusive subunits with high degrees of modularity in the best-supported hypothesis of modularity. Yet, this is not the case as seen in the relatively poorly supported modular hypothesis M3a of both trilobite species examined (Figures 2 and 4). It is notable that function was also a poor predictor of modularity in previous studies of early Cambrian trilobite cranidia though development was not rigorously assessed in this case (Webster & Zelditch, 2011a, 2011b). Ultimately, however, attempting to decouple development and function in terms of subunits of the head is difficult and it may be much more fruitful to consider function and development as inseparable but not irreconcilable. For example, an influential hypothesis of modularity in the vertebrate cranium considers each subunit to be simultaneously a developmental and functional module (Cheverud, 1996; Zelditch & Goswami, 2021). Development is encompassed within the function as theoretically “developmental processes serve a functional role and function is a developmental

**FIGURE 6** Diagrams of the M5b modular hypothesis of (a) *Calyptaulax annulata* and (b) *Calyptaulax senilis* with colors corresponding to the pairwise CR value between the eyes and each respective partition of the cranidium. Regions are color-coded according to the pairwise CR value between that region and the eye partition (black). In both species, the anteriormost region of the cranidium has the highest CR value and therefore the strongest association with the eyes.
process” (Zelditch & Goswami, 2021). In this study, this approach would be manifest in the acknowledgment that while the eyes serve an obvious functional purpose, they also have well-supported developmental correspondence in the trilobite head.

The number of segments in the euarthropod head varied among the earliest groups (Ortega-Hernández et al., 2017; Richter et al., 2013). Within total-group Euarthropoda, the Cambrian fossil record captures a single segmented head (in lower stem-group euarthropods), a three-segmented head (in upper stem euarthropods), and a five (or more) segmented head (in euarthropods such as trilobites) (Ortega-Hernández et al., 2017). Though debate remains on the segmental homology of the head region in Euarthropoda, there is consensus that the eyes are derived from the protocerebral segment (Bergström, 1973a, 1973b; Henriksen, 1926; Lev et al., 2022; Ortega-Hernández et al., 2017; Størmer, 1942). This anteriormost ocular segment provides a stable reference point to trace the accumulation of segments in the euarthropod head, and it has been proposed that a critical feature in the evolutionary history of Euarthropoda was the iterative recruitment of segments into the head from the trunk region (Ortega-Hernández et al., 2017). As shown in this study, patterns of covariation between and within regions of the head are not equal. The integration of the euarthropod head as a unit may have been driven by functional pressures with patterns of covariation in subunits shifting gradually. This process may be related to the “imitatory epigenotype” hypothesis where traits (or segments in this case) that are functionally interdependent become developmentally linked and integrated into the head (Riedl, 1978). More recently, however, it has been proposed that the multi-segmented head in arthropods is derived from the division of the anteriormost segment (Lev et al., 2022). In theory, these hypotheses could be tested by examining patterns of modularity in the (unfused) euarthropod head. In contrast to stem euarthropods, the number of segments in the trilobite head appears to have been stable despite dorsal expression of segmentation being variable particularly in the glabella. This stability may be related to the dorsal exoskeleton fusion of segments observed in crown Euarthropoda. Furthermore, this stability extends to broad patterns of covariation as observed in the two distantly related trilobite species within this study.

That patterns of modularity are consistent in these species belonging to different orders of Trilobita raises the question of whether modularity patterns were conserved in trilobites as a whole. If this was the case, then modularity could have had significant macroevolutionary consequences over the evolutionary history of trilobites (Goswami et al., 2014, 2015). The developmental coupling of the eyes with the anteriormost region of the cranidium may have imposed a constraint on patterns of diversification that may have either impeded or enhanced the rate of evolution depending on its congruence with selective pressures (Simpson, 1944). Rigorous assessment of this will require further study of modularity across trilobite groups throughout the Paleozoic.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available as supplementary material. Upon acceptance, data will also be deposited in and openly available from the AMNH Library Digital Repository at https://doi.org/10.5531/sd.paleo.9

ORCID
Ernesto E. Vargas-Parra https://orcid.org/0000-0002-4773-6811

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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