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Homeotic evolution in Cambrian trilobites

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Abstract.—Hox genes are known from a wide variety of organisms. In arthropods, these genes control segment characteristics. Trilobites, being arthropods, probably contained eight major Hox genes that controlled their segment types. The trilobite Bauplan contains eight regions that are most likely under the influence of one or more of these Hox genes. The cephalon contains the frontal lobe, glabellar, and occipital ring regions; the thorax contains the anterior thoracic and posterior thoracic regions; and the pygidium contains the articulating ring, axial, and terminal piece regions. Changes in character distribution within or between these regions represent homeotic evolution, which may have resulted from the modification of Hox transcription or of downstream regulatory genes. A phylogenetic analysis is used to recognize homeotic evolution in trilobites, leading to the conclusion that homeotic evolution is common among Cambrian trilobites.

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Introduction

The importance of Hox and other regulatory genes in a wide variety of metazoans has received broad recognition by neontologists. Hox genes control the differentiation of segments during arthropod development (Raff and Kaufman 1983; Raff 1996). Mutation of these genes, or ''upstream'' genes affecting Hox genes, or ''downstream'' regulatory genes affected by the Hox genes can result in the transfer of a morphological feature typical of one body region to another. For example, in fruit flies (*Drosophila*), experimental manipulation of Hox genes has produced homeotic change, with the generation of legs where mouthparts or antennae belong or two pairs of wings instead of a pair of wings and halteres (Raff and Kaufman 1983; Pultz et al. 1988; Lawrence 1992). Mutations affecting the Hox genes may be involved in the homeotic evolution of some higher taxa, including several groups within the arthropods (e.g., onychophorans, myriapods, insects, and crustaceans [Raff and Kaufman 1983; Jacobs 1987, 1990; Akam et al. 1994; Whiting and Wheeler 1994; Carroll 1995; Raff 1996; Averof and Patel 1997; Grenier et al. 1997]).

Paleontologists, however, are only beginning to realize the importance of regulatory genes in evolution. Some have suggested that these genes played an important role in the Cambrian explosion and in the evolution of several Cambrian arthropod taxa (Jacobs 1987, 1990; Valentine et al. 1999; Erwin 1999). The intent of this paper is to illustrate that homeotic evolution was an important mode of evolution for species and genera and not just for the origin of major groups. I will illustrate that repetitive morphological features of several specific regions of trilobite Bauplan where probably controlled by Hox genes and that homeotic evolution was an important mode of evolution in Cambrian trilobites.

Definitions

Because of potential confusion between homeotic change, homeotic mutations, and homeotic evolution, the following definitions will be used:

1. *Homeotic change* (or homeotic transformation)—the transfer of a feature typical of one region or segment to another body region or segment. Homeotic change is purely a descriptive term not implying a precise mechanism for transformation. This change can result from either the mutation of Hox genes, ''upstream'' changes that affect Hox gene interaction with other genes (Lewis 1978; Manak and Scott 1994), or ''downstream'' regulatory genes that are target genes for Hox genes (Carroll 1994, 1995; also see Budd 1999). Homeotic change can also result from mutation

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of other homeobox genes not associated with the Hox clusters (e.g., *trithorax, extradenticle, buttonhead, orthodenticle, empty spiracles, Distal-less* [Manak and Scott 1994 and references therein]). In some cases, homeotic changes can result from environmental conditions (Raff and Kaufman 1983; Lawrence 1992).

2. *Homeotic mutation*—a genetic mutation that causes a homeotic change.

3. *Homeotic evolution*—the transfer of a feature typical of the ancestor's body region or segment to another body region or segment of its descendant. Homeotic evolution takes place when a homeotic change is heritable (i.e., through homeotic mutation).

Homeotic Change

Most discussions of homeotic changes in arthropods have focused on either the distribution or presence of appendage and wing types (e.g., Raff and Kaufman 1983; Jacobs 1987, 1990; Pultz et al. 1988; Akam et al. 1994; Whiting and Wheeler 1994; Carroll 1995; Lawrence 1992; Raff 1996; Averof and Patel 1997), but homeotic changes are not limited to just appendages and wings. Other morphologies are influenced by Hox genes, such as muscle types, sternites, ventral setal bands, Wheeler's Organ, anterior spiracles, Keilin's Organs, and tracheal sections of the dorsal longitudinal trunk (Lewis 1978; Raff and Kaufman 1983; Hooper 1986; Casanova et al. 1988). This is an important point to make, for trilobites have relatively uniform biramous appendages (and no wings), with the exception of the uniramous antennae and the occasional uniramous antennioform cerci (Harrington in Harrington et al. 1959). Limb uniformity indicates that homeotic changes did not have a dramatic effect on the limb construction or distribution like that illustrated or hypothesized for other arthropods.

Many of the homeotic changes described below are relatively minor and not wholesale transformations. But homeotic changes are not necessarily global; the entire set of segment characteristics needs not be transferred from one region to another. For example, gradational or partial changes in segment character have been documented in *Drosophila* (Lewis 1978; Casanova et al. 1988; Lawrence 1992). These gradational or partial changes are expected because the entire set of segmental characteristics is determined by more than one Hox gene (Lewis 1978; Raff and Kaufman 1983; Lawrence 1992; Manak and Scott 1994). Minor morphological changes could also result from the mutation in the binding sites of a target gene that allowed different Hox genes to bind (Lawrence 1992; also see Carroll 1995). If this downstream gene is also a regulatory gene, then a preexisting morphological character could have a new distribution among segments (a level 4 change of Gellon and McGinnis 1998).

Trilobites Are Like the Rest

Hughes and Chapman (1995) suggested that trilobites contained Hox genes because Hox genes are found in a wide variety of animals ranging from hydra, nematodes, priapulids, annelids, brachiopods, onychophora, arthropods, to chordates (Akam et al. 1994; Carroll 1995; Raff 1996; Averof and Patel 1997; Grenier et al. 1997; Rosa et al. 1999). Given the phylogenetic reconstruction of Annelida, Onychophora, and Arthropoda (Wills et al. 1994, 1997), trilobites contained all eight major Hox genes. Annelids contain five Hox genes that are orthologues to those found in *Drosophila*: *labial* (*lab*), *proboscipedia* (*pb*), *Deformed* (*Dfd*); *Antennapedia* (*Antp*), and *Ultrabithorax* (*Ubx*)/*abdominal A* (*abd-A*)-like gene (Dick and Buss 1994; Snow and Buss 1994). Four other Hox genes—*Sex comb reduced* (*Scr*), *Abdominal B* (*Abd-B*), *abd-A,* and *Ubx* (the latter two replacing the *Ubx*/*adb-A*–like gene listed above)—are found as orthologues in onychophorans (Grenier et al. 1997). In other words, trilobites probably had at least eight Hox genes because this condition is plesiomorphic to the onychophoran/arthropod clade (Rosa et al. 1999).

The cheilicerate *Limulus,* which belongs to the sister group of trilobites, contain either orthologues or paralogues of at least seven Hox genes (Cartwright et al. 1993). *Scr,* which is found in Onychophora, Hexopoda, Crustacea, and vertebrates (Carroll 1995; Grenier et al. 1997), has not been recognized in *Limulus.* In addition, *Limulus* are reported to have four clusters of Hox genes (Cartwright et al. 1993) instead of the single cluster found in mollusks, annelids, crustaceans, and hexapods (Dick 1997). Whether this Hox configuration is unique to just *Limulus,* or to all chelicerates or arachnomorphs (which includes the trilobites), is unknown.

Hox genes determine segment identity in *Drosophila* (Lawrence 1992; Raff 1996). *Lab, pb,* and *Dfd* regulate head segments; *Scr, Antp,* and *Ubx* regulate thoracic segments; and *abd-A* and *Abd-B* regulate abdominal segments. Because these genes are also found in a wide variety of arthropods and onychophora (Carroll 1995; Grenier et al. 1997), we can use the "phyletic phenocopy paradigm" (where differences ascribable to mutant phenotypes in model taxa are expanded in the context of phylogeny [see Stebbins and Basile 1986; DeSalle and Carew 1992]) to say that Hox genes controlled the character of segments within the major body sections of other arthropods including trilobites. Averof and Patel (1997) have documented this genetic control in crustacean limb development. However, the morphologic expression of these genes or even the body regions influenced by these genes are not the same among all phyla (Carroll 1995; Raff 1996), or even among all arthropods (Carroll 1995; Averof and Patel 1997) or insects (Akam et al. 1994). For example, crustaceans display a slightly different pattern, with *Ubx* and *abd-A* expressed in nearly all limb-bearing thoracic segments (Carroll 1995; Averof and Patel 1997).

Trilobite Bauplan

Expression of individual Hox genes in trilobites is probably restricted to smaller regions of the cephalon, thorax, and pygidium. These smaller regions are based on the grouping of similar segments within each tagma (Fig. 1). An individual Hox gene or interactions between Hox genes may help determine the morphology of one or more of these regions. Consequently, changes in serial characters of these smaller regions can indicate homeotic evolution. The cephalon can be divided into three regions: (1) frontal lobe region, including the anteriormost lateral glabellar furrow and probably the extraocular region; (2) glabellar region, which probably includes the interocular region; and (3) occipital ring region, including the posterior border and furrow. The presence or absence of axial nodes, axial spines, or long pleural spines in the thorax suggests anterior and posterior thoracic regions. The redlichiids *Olenellus* (*Paedeumias*) *chiefensis* and *O.* (*P.*) *terminatus,* both described by Palmer (1998), lack axial nodes or spines on the first to ninth thoracic segments; but, they are present on the tenth to fourteenth thoracic segments. The ptychopariid *Marjumia typicalis* (Resser) has a similar subdivision of the thorax, as evidenced by the difference in pleural spine lengths between the first eleven thoracic segments and the last three segments (Fig. 8A). The pygidium is also divided into three regions that parallel in reverse order the regions of the cephalon: (1) articulating ring region, including the anteriormost axial ring and anterior and posterior pleural bands; (2) axial region, including the remaining axial rings and adjacent pleural field; and (3) terminal piece region, which includes the post-axial area of the pleural field.

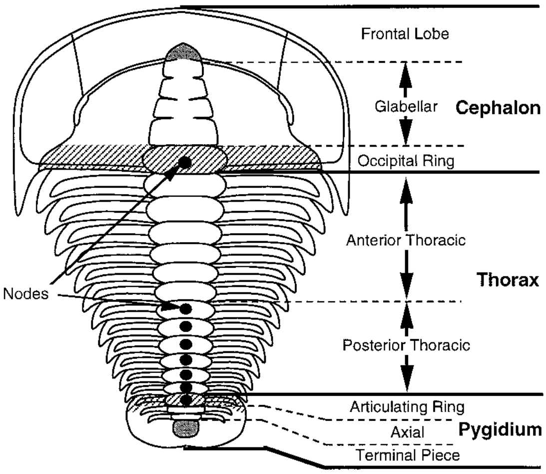

FIGURE 1. Regions of trilobite Bauplan where segment characteristics are probably controlled by Hox genes.

A one-to-one correlation of exoskeleton segmentation to body stomites in trilobites is assumed (see Sundberg 1995). Thus, the regions defined above are thought to correlate to ventral and internal body regions as well.

Transitional Morphologies between the Major Body Sections

The occipital ring region of the cephalon and articulating ring region of the pygidium

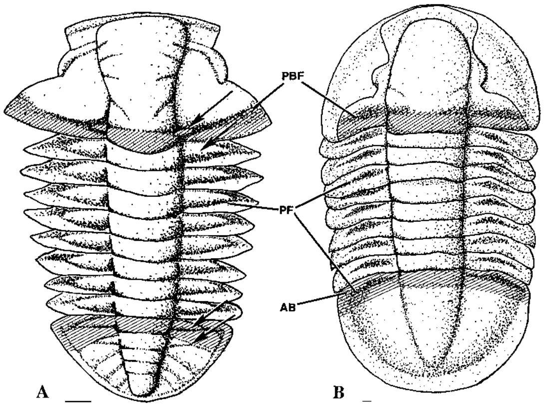

FIGURE 2. Trilobites illustrating similarities between adjacent regions. Anterior shaded area is the occipital ring region and posterior shaded region is the articulating ring region. A, *Klotziella ornata* (Walcott) (drawn from Rasetti 1951: Plate 28, Figs. 7, 8), illustrating the similarity in segment character between the occipital ring and thoracic regions. The triangular raised areas (arrows) adjacent to the occipital ring, axial rings, and first two pygidial rings are a unique configuration. More normal configuration of these regions is illustrated in Figure 2B. B, *Niobella aurora* (Westargård) (drawn from Levi-Setti 1993: Plate 113), illustrating the similarity in segment characters between the articulating ring region of the pygidium and the posterior thoracic region. Scale bar, 1 mm. PF = pleural furrow, PBF = posterior border furrow, AB = anterior pleural band.

(Fig. 1) have characteristics typical of the adjacent regions. *Klotziella ornata* (Walcott) (Fig. 2A) provides a good example of the transitional morphology of the occipital ring region between the glabellar and thoracic regions. In the occipital ring region, the posterior border furrow is directed anterolaterally and the lateral portion of the occipital ring forms a small, raised triangular area on the anterior edge of the posterior border furrow. This is a unique configuration for trilobites, which typically have the posterior borders directed laterally or posterolaterally and have rounded projections of the occipital ring (e.g., Fig. 2B). This unique configuration is also present in each thoracic segment and the first two pygidial segments. The anterolateral furrows or triangular shapes are not present in the glabellar region or the remaining portion of the pygidium. *Aciculolenus palmeria* Chatterton and Ludvigsen (1998: Fig. 14) is another example of intermediate morphology between the two regions with its long intergenal spine identical to its thoracic pleural spines.

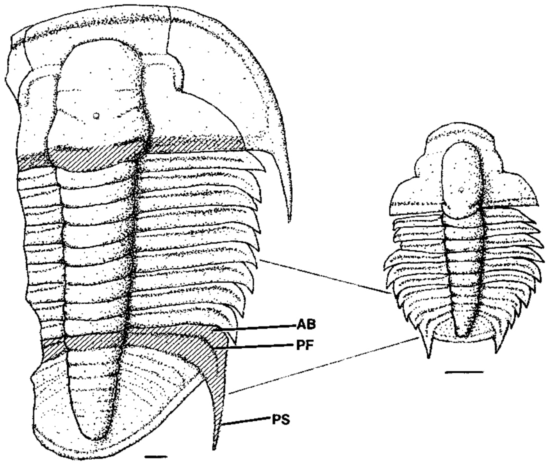

FIGURE 3. *Proceratopyge* (*Lopnorites*) *rectispinatus* (Troedsson) (drawn from Palmer 1968: Plate 10, Figs. 1, 3, 4; larger specimen has been inverted from the original photograph), illustrating the similarity in segment character between the articulating ring and thoracic regions. The sixth-degree meraspis illustrates that segment characteristics are defined prior to final tagmosis of the pygidium. Scale bar, 1 mm. PF = pleural furrow, PS = pleural spine, AB = anterior pleural band. Anterior shaded area is the occipital ring region and posterior shaded region is the articulating ring region.

The articulating ring region of the pygidium is most similar to the thoracic regions. This pygidial region typically has well-developed axial rings and well-developed pleural furrows and anterior pleural bands that extend to or near the pygidial margin. The similarity is most visible on species that have a pleural spine on the first segment of the pygidium, as in *Proceratopyge* (*Lopnorites*) *rectispinatus* (Troedsson) (Fig. 3), or where the remaining portion of the pygidium is effaced, as in *Niobella aurora* (Westargård) (Fig. 2B) or *Plethopeltis armatus* (Billings), illustrated by Ludvigsen et al. (1989: Plate 45, Figs. 10, 11). In *P.* (*L.*) *rectispinatus,* the character of the last three thoracic segments and the first pygidial segment is defined when they are part of the transitory pygidium. This indicates that the characters of these segments are defined before they are released from the pygidium into the thorax and not the result of the release itself.

Homeotic Evolution of Cambrian Trilobites

In this study, homeotic change is indicated by distribution changes of characters among body segments. Only Cambrian trilobites are used here to provide examples of homeotic evolution, although post-Cambrian trilobites probably also display homeotic evolution. These examples of homeotic change may result from mutation of either Hox genes, upstream genes that either directly regulate the Hox genes or suppress expression of segment characteristics, or downstream genes affected by the Hox genes (Carroll 1994, 1995; Raff 1996; Gellon and McGinnis 1998). However, the mutation type that caused a specific case of homeotic evolution can be firmly established only when using modern organisms (e.g., Averof and Patel 1997). Therefore, when a homeotic change is observed in trilobites it cannot be assigned to a specific mutation in the genome.

Homeotic Evolution versus Heterochrony

McNamara (1986) proposed that heterochrony was a significant factor in the evolution of Cambrian trilobites. I propose here that homeotic evolution was common in Cambrian trilobites. Both homeotic change and heterochrony are descriptive terms—they describe how a descendant resembles its ancestor. In homeotic evolution, the proportion of segments containing certain characters has changed. If the segment character is either (1) deleted from one region, making it similar to other regions, yet maintained in another region or (2) propagated to a new region, then the change represents homeotic evolution. For example, if a trilobite has pygidial spines and it is derived from a species that has thoracic pleural spines and no pygidial spines, then the pygidial regions have obtained a characteristic of the thoracic region. In heterochrony, the descendant can have the retention of juvenile features (paedomorphism) or the progression of features (peramorphism) beyond the range of its ancestor. If a segment character (e.g., pleural spines) is present within a region at some time during the ancestor's ontogeny, then the propagation or reduction of this character within the region is a heterochronic change.

However, in some instances there is no clear separation between heterochrony and homeotic evolution. Heterochronic changes can be the result of changes in Hox genes (Raff 1996), thereby resulting in homeotic changes. In addition, some Hox genes may be expressed only in specific ontogenetic stages (Pultz et al. 1988; Castelli-Gair et al. 1994; Castelli-Gair and Akam 1995); thus, homeotic changes could result from heterochronic changes. For example, if the ancestor is generating pleural spines during the formation of both the thorax and pygidium, and the descendant generates spines only during the formation of the thorax, then the Hox gene that regulated the formation of the spines was "turned off" during an earlier growth stage before the pygidium was formed. However, mechanisms exist that maintain the effects of Hox genes even after their disappearance from cells (see Manak and Scott 1994).

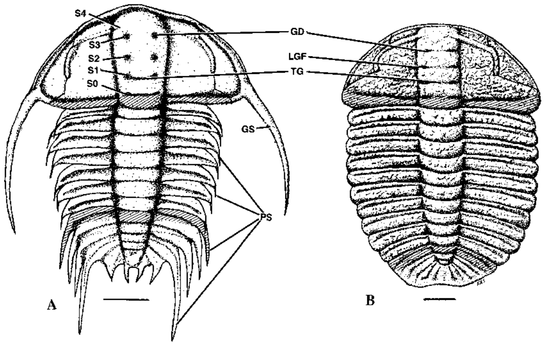

FIGURE 4. Representatives of Oryctocephalidae. A, *Oryctocephalites walcotti* (Walcott) (drawn from Campbell 1974), belonging to Oryctocephalinae. B, *Arthricocephalus chauveaui* Bergeron (drawn from Chang et al. 1980: Plate 94, Fig. 1), belonging to Oryctocarinae. Scale bar, 1 mm. Anterior shaded area is the occipital ring region and posterior shaded region is the articulating ring region. GD = glabellar depression, GS = genal spine, LGF = lateral glabellar furrow, PS = pleural spine, S0 to S4 = lateral glabellar furrow positions (even when not present), TG = transglabellar furrow.

Oryctocephalids

Homeotic changes of cephalic limbs, or at least their muscle attachments, are well illustrated by the Oryctocephalidae (Corynexochida). The oryctocephalids (Fig. 4) vary in the shape of glabellar depressions and number of lateral glabellar and transglabellar furrows. These features represent apodemes that function as muscle attachments for appendages (Harrington *in* Harrington et al. 1959; Bergström 1973; Cisne 1975). Changes in the de-

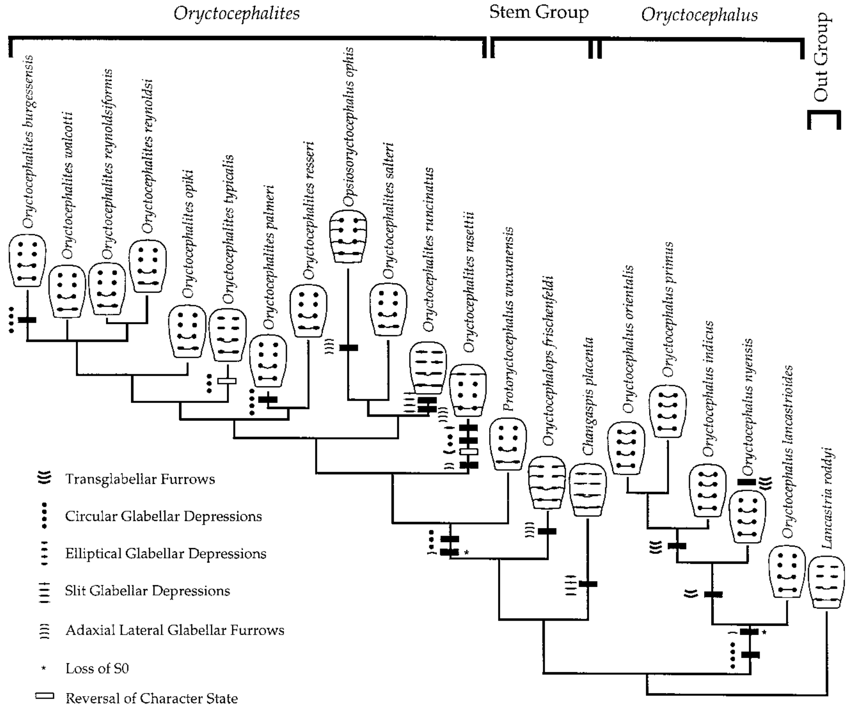

FIGURE 5. Phylogram of Oryctocephalinae illustrating character changes resulting from homeotic evolution. The number of symbols represents the number of lateral glabellar or transglabellar furrows for each node where the counts change. The solid bar above the glabellar representation of *Oryctocephalus nyensis* represents a polymorphism of two or three transglabellar furrows. Phylogram from Sundberg and McCollum 1997.

pression shapes or furrow number reflect changes in appendage muscles and possibly differences in limb structure.

Using an explicit phylogenetic hypothesis for the spiny oryctocephalids (Oryctocephalinae; Fig. 4A) from Sundberg and McCollum 1997 (Fig. 5), 18 instances of homeotic evolution can be identified. The number of transglabellar furrows changed four times and is most variable in *Oryctocephalus*; *O. nyensis* is polymorphic with either two or three transglabellar furrows. The shape of the glabellar depressions changed nine times and the extension of the lateral glabellar furrows to the axial furrows changed five times.

This phylogram uses 36 characters, including the transglabellar furrows, depression shape, and lateral glabellar furrows as characters. By including these three characters, the amount of homoplasy and homeotic change is potentially reduced because those taxa with similar character states would tend to cluster together. This study subdivides the shape of the glabellar depressions into three states: slit shaped, elliptical, and circular. However, for the construction of the phylogram (Sundberg and McCollum 1997), the elliptical and circular depression shapes were assigned to the same state because they can be distorted through tectonic activity.

The transglabellar furrows within *Oryctocephalus* show a progressive addition in occurrence from the occipital ring region to the posterior and then anterior portions of the glabellar region. These changes are most similar to the posterior-to-anterior shift of muscle arrangement observed in *Drosophila* that resulted from the homeotic mutation of the *Ubx* complex (Hooper 1986).

Preservation Problems.—Oryctocephalid trilobites are typically found in deeper-water, offshore shales of the craton margin. As a result, most oryctocephalids are compressed in shales, which could influence the presence or absence of the transglabellar furrows, shape of the glabellar depressions, and the presence of lateral glabellar furrows. To determine this influence, meraspides and holaspides of *Or-*

yctocephalites walcotti Resser ($n = 87$), *O.* cf. *typicalis* Resser ($n = 28$), and *Oryctocara geikiei* Walcott (Oryctocarinae) ($n = 12$) from the Middle Cambrian Spence Shale were studied. These specimens consist only of molds and casts, typically with an authogenic mica present. No tectonic distortion of the specimens was evident. Positive and negative impressions of several different sizes were studied. The location and shape of the glabellar depression, location of transglabellar and glabellar furrows, and cranidial length were recorded for each specimen.

The results for *Oryctocephalites walcotti* are illustrated in Figure 6. *Oryctocephalites walcotti* has elliptical glabellar depressions at the S0 (occipital ring furrow), circular depressions at the S1–S3 positions, transglabellar furrows at the S0 and S1 positions, and lateral glabellar furrows at the S4 position (Fig. 4A). When either the S2 or S3 transglabellar furrows are not clearly compression cracks but possibly the result of compression, the box received a gray shade. When the shape of the glabellar depression could not be accurately determined because of compression or preservation, the depression shape is recorded as an open circle or ellipse.

The results illustrate that the shape of glabellar depressions and presence of transglabellar furrows are consistent through development and compression. The shapes of the S0 glabellar depressions were difficult to determine only in the smallest specimens (<1.6 mm; see below). Only a few specimens deviated from the ''standard'' form given above, and most of these are questionable and could have resulted from compression (gray boxes). Two examples (2.0–2.2 mm and 3.0–3.2 mm, both in the first row) are notable exceptions, they have well-developed transglabellar furrows not only at the S0 and S1, but also at S2 and S3 positions. Another specimen (5.6–5.8 mm, second row) has the transglabellar furrow missing in the S1 position. These rare occurrences represent homeotic change within the species.

In addition, although not presented on Figure 6, the number and location of the lateral glabellar furrows are also consistent in the larger specimens (see below).

Similar results were obtained for *Oryctocephalites* cf. *typicalis* and *Oryctocara geikiei.* The glabellar depression shape and location of transglabellar furrows were constant, with only a few questionable deviations from the ''standard'' forms. This study suggests that compression does not mask these individual characters.

Homeotic Evolution versus Heterochrony Revisited.—Meraspides and holaspides of *Oryctocephalites walcotti, O.* cf. *typicalis,* and *Oryctocara geikiei* typically do not display ontogenetic changes of the character states discussed above. Meraspides of *Oryctocephalus indicus* (Reed) (redescribed in Sundberg and McCollum 1997) also show no ontogenetic change in these characters (Sundberg unpublished data). Because these oryctocephalids are generally consistent in the number or shape of glabellar depression, transglabellar furrows, and lateral glabellar furrows during ontogeny, specific changes in these features do not represent heterochrony.

The smallest specimens of *Oryctocephalites walcotti* are an exception. The elliptical depressions in the occipital ring furrow (S0) of this species appear to be slit shaped in cephalon sizes between 0. 8 and 1.4 mm (Fig. 6), although the slit shape could not be firmly established and can be the result of preservation (see above). The adaxial portion of the occipital furrow (S0) in these smaller specimens is present, indicating an ontogenetic loss of this feature in holaspides. These results indicate that heterochrony may be responsible for the changes in depression shape and in the adaxial furrows for the occipital ring region, but not for observed changes to the anterior.

Other Trilobite Groups.—The cranidia of Oryctocephalinae provide us with a set of unique morphologic characters that illustrate homeotic evolution. Other trilobites possess some of these cranidial features, although no other group has all three characters developed as extensively. Glabellar depressions are present in ptychopariids (Phacopina, Olenacea) and redlichiids (Olenellina, Redlichiina). Transglabellar furrows are common among the redlichiids (Olenellina, Redlichiina, Bathynotina), but rare among the ptychopariids (Ptychaspidacea). Lateral glabellar furrows do not con-

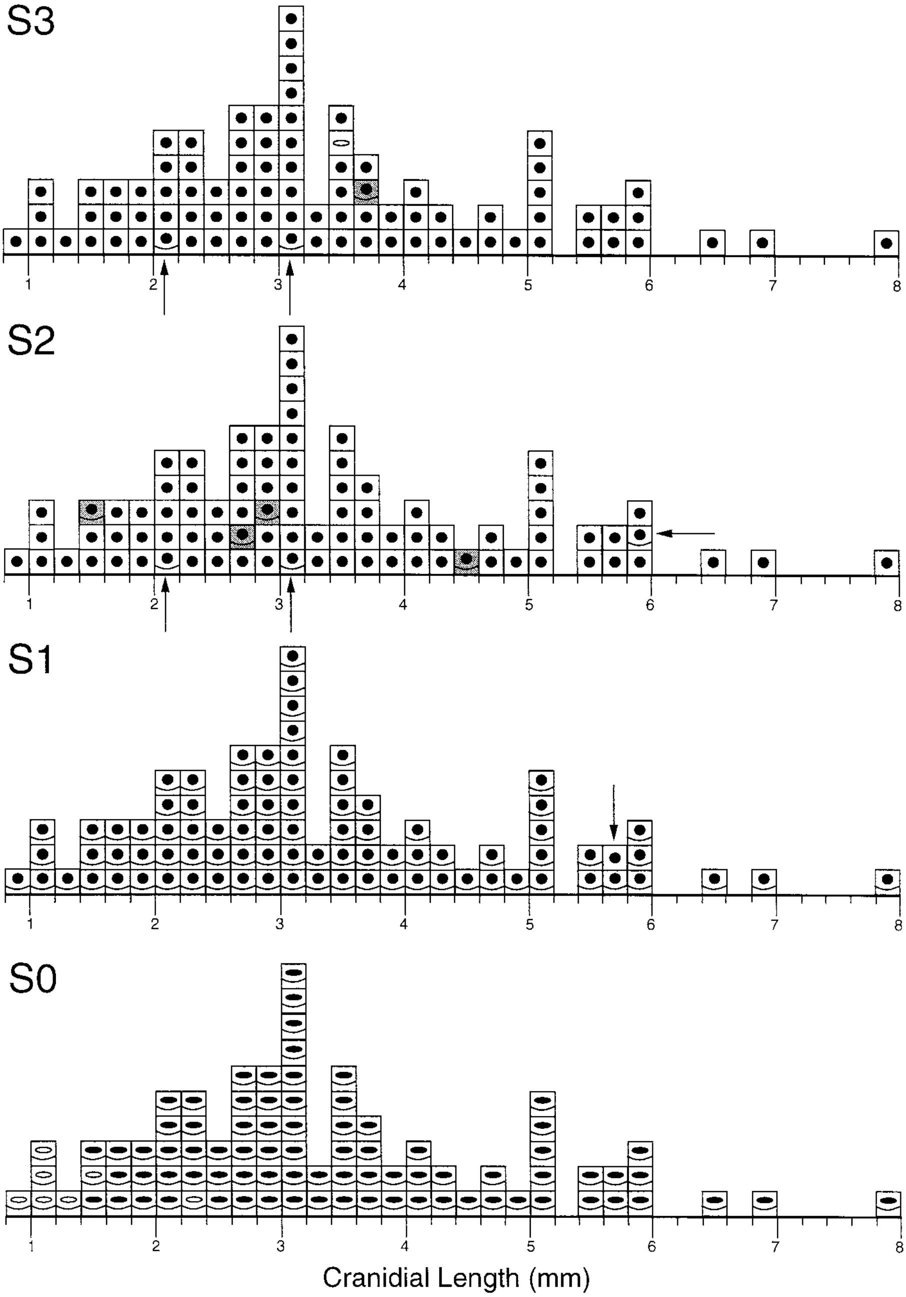

FIGURE 6. Histograms illustrating the presence or absence of transglabellar furrows (curved line) or circular or elliptical glabellar depressions (circles or ellipses) in individual specimens of *Oryctocephalites walcotti*. Individual specimens are represented as a box in the same position in each histogram. The curved line in a box indicates the presence of a transglabellar furrow in that specimen at that glabellar position (S0–S3). Gray boxes indicate questionable presence of transglabellar furrows due to preservation. Circles or ellipses indicate the glabellar depression shape in that specimen at the position. Solid circles/ellipses indicate positive identification of depression shape, and open circles/ellipses indicate questionable identifications due to preservation. Arrows indicate specimens that deviate from the "standard" form of the species.

nect with the axial furrows in several ptychopariids (some Phacopina, Proetacea, Ceratopygacea, Remopleuridacea, Anomocaracea, Olenacea) and redlichiids (Olenellina, Redlichiina). Oryctocephalids are unique among the corynexochids in possessing these glabellar characters. A precursory survey suggests that good examples of homeotic evolution of these glabellar characteristics are present within the redlichiids (Olenellina, Redlichiina) and ptychopariids (Olenacea).

Axial Nodes

Axial nodes or spines are common on several trilobites, including some redlichiids (Ellipsocephalidae, Olenellina, Redlichiina), corynexochids (Dolichometopidae, Dorypygidae, Zacanthoididae), and ptychopariids (e.g., Alokistocaridae, Cedariiidae, Dikelocephalidae, Idahoiidae, Marumiidae, Parabolinoididae, Ptychpariacea, Saukiidae). These nodes occur on the axial rings of the occipital ring, anterior thoracic, posterior thoracic, articulating ring, and/or axial regions. Distribution changes in these nodes represent a homeotic change. For example, an ancestor could have a node on the occipital ring and its descendant have nodes on the occipital ring and thoracic rings, indicating the thoracic segment's acquisition of the occipital ring feature.

Perhaps the most interesting distribution of nodes is seen in *Nephrolenellus multinodus* (Palmer). This species is unlike any other olenellid in its possession of axial nodes in the occipital ring and glabellar regions (Fig. 7A). The stratigraphically younger *Nephrolenellus geniculatus* Palmer generally lacks the nodes on the glabellar region (Fig. 7B), although the smaller specimens do have a complete set of axial nodes (M. Webster personal communication 1999). If the younger *Nephrolenellus* is the descendant of the older species, then two homeotic changes have occurred: the glabellar region acquired the node typical of the occipital ring region in *N. multinodus,* and then this feature was lost in *N. geniculatus.* This node loss appears to be tied to a heterochronic change as well.

Palmer and Repina (1993 and figures therein) provide various examples of homeotic change in the distribution of axial nodes in olenellids. Several species have no axial nodes on the thoracic segments (e.g., in Fig. 4, *Biceratops nevadensis* Pack and Gayle, *Peachella iddingsi* [Walcott], *Bristolia bristolensis* [Resser]). Some species have nodes on all thoracic segments (e.g., in Fig. 3, *Mummaspis occidens* [Walcott] *Olenellus* (*Olenellus*) *thompsoni* [Hall], and *Olenellus* (*Mesolenellus*) *hyperborea* [Poulsen]). Still others have nodes on only the posterior thoracic segments (e.g., in Figs. 3 and 4, *Olenellus* (*Paedeumias*) *transistans* [Walcott] and *Gabriellus* sp.). Lieberman (1998) considered the presence of axial nodes as plesiomorphic (his character 66, state 0). The disappearance of all axial nodes on the thorax occurs four times on his cladogram of the olenellids (character 66, state 1). Axial nodes are present only on the posterior thoracic region two times on the cladogram (listed as character 66, state 0). The disappearance of axial nodes from either some or all thoracic segments and their persistence on the occipital ring (Lieberman 1998, character 40, state 1 or 2) represents homeotic evolution within the Olenellinae. The number

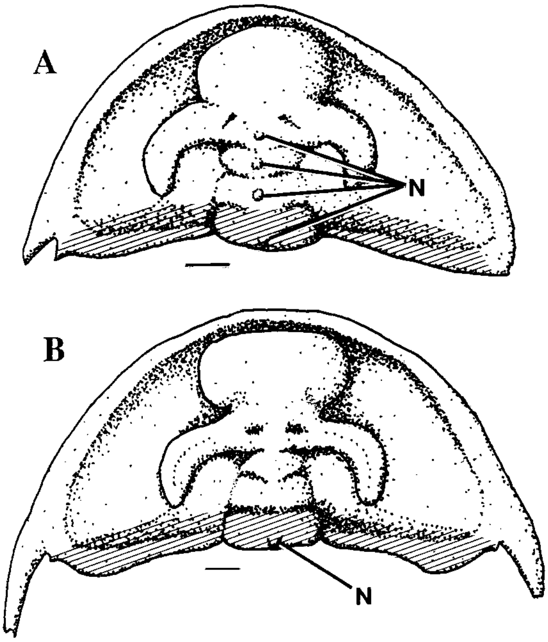

FIGURE 7. Specimens of *Nephrolenellus* showing differences in node (N) distribution in the glabellar and occipital ring regions. A, *Nephrolenellus multinodus* (Palmer), drawn from Palmer and Repina 1993: Fig. 4.4. B, *Nephrolenellus geniculatus* Palmer, drawn from Palmer 1998: Fig. 6.1. Scale bar, 1 mm. Shaded region represents the occipital ring region.

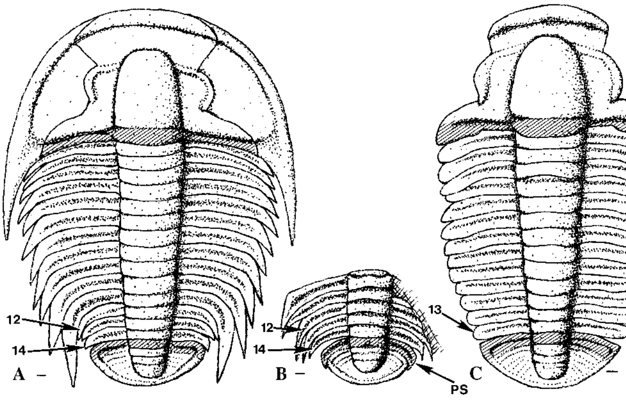

FIGURE 8. Specimens of *Marjumia* showing differences in pleural spines and pygidial spines. A, *Marjumia typicalis* (Resser), drawn from Levi-Setti 1993: Plate 107. B, Pygidium and thoracic segments of *Marjumia masoni* (Resser), drawn from unpublished figure. C, *Marjumia laevinucha* Robison, drawn from Robison 1971: Plate 90, Figs. 11–13. Scale bar, 1 mm. Anterior shaded area is the occipital ring region and posterior shaded region is the articulating ring region. Specific thoracic segments are numbered. PS = pleural spine.

of episodes of homeotic evolution within the Olenellinae is difficult to determine because Lieberman (1998) used only one representative of each genus in his cladistic analysis. Node appearance on thoracic segments is variable within genera as well as between genera (see Palmer 1998).

Pleural Spines

Several trilobite groups also display homeotic evolution in the distribution of pleural and genal spines. Oryctocephalidae not only have the typically spiny forms that were discussed above (Oryctocephalinae, Fig. 4A), but also nonspiny forms (Oryctocarinae, Fig. 4B). The spiny forms typically have long genal, thoracic, and pygidial spines. A few taxa in Oryctocarinae have lost some of these spines. For example, *Oryctocara ovata* Tchernysheva (1962: Plate 4) has small pointed terminations of the thoracic segments but lacks genal and pygidial spines. *Tonkinella* also has small pointed terminations of the thoracic segments but possesses long genal spines much like Oryctocephalinae (see Rasetti 1951: Plate 31, Fig. 14). Other members of Oryctocarinae have lost all spines, for example, *Arthricocephalus chauveaui* Bergeron (Fig. 4B), *Oryctocara geikiei* (Walcott) (see Whittington 1995: Plate 4), and *Sandoveria lobata* Shergold (1969: Fig. 14). This progressive loss of spines probably represents homeotic evolution, although the phylogeny of this group needs to be worked out before the number of episodes can be determined. In addition, the nonspiny Oryctocarinae are variable in the number and/or shape of the transglabellar furrows, glabellar depressions, and lateral glabellar furrows, as are the spiny Oryctocephalinae, and probably display homeotic evolution in these characters.

The presence of pygidial spines in some species of *Marjumia* (Marjumiidae, Ptychopariida) and their absence in other species (previously assigned to *Modocia* [Melzak and Westrop 1994]) (Fig. 8) provides another example of homeotic evolution. These pygidial spines are the propagation of thorax type spines onto the pygidial regions and not the fusion of a thoracic segment to the pygidium. If the pygidial spines resulted from the retention of thoracic segments within the pygidium, then the spiny taxa should have fewer thoracic segments and more pygidial segments. Taxa that lack pygidial spines have 12 to 14 thoracic segments and 3 to 4 pygidial axial rings (Robison 1964, 1971; Schwimmer 1973). However, the spiny species has 14 thoracic segments and 3 to 4 pygidial axial rings (Robison 1964), and thus the presence of the pygidial spines is the result of homeotic change. If thoracic segments were being retained in the pygidium, then forms of *Marjumia* with only 13 thoracic segments should have a set of pygidial spines, which they do not (Fig. 8C).

Lengths of thoracic pleural spines also vary within *Marjumia*. *Marjumia typicalis* (Resser;

Fig. 8A) has long pleural spines, increasing in length from the first to the eleventh thoracic segment (anterior thoracic region) and much smaller pleural spines on the twelfth to fourteenth segments (posterior thoracic region). *Marjumia masoni* (Resser) has a similar increase in pleural spine length, but the last four thoracic segments decrease in size gradually and the first pygidial segment has a small spine and looks much like a thoracic segment (Fig. 8B). Both species differ from *M. laevinucha* Robison (1971) (Fig. 8C) and *M. brevispina* Robison (1964: Plate 87, Figs. 11–19), which have only rounded pleural terminations.

Discussion

The taxonomic importance of the characters discussed above for Cambrian trilobites is limited. Taken by themselves, homeotic changes in glabellar depressions, transglabellar furrows, lateral glabellar furrows, pleural spines, and axial nodes are used to define different species or genera, but not higher taxa. On the other hand, thoracic segment types (prothoracic versus opithothoracic segments) and the presence or absence of genal spines are used to help differentiate two subfamilies of Olenellina (see Palmer and Repina 1993). The depth of lateral glabellar furrows, the presence of thoracic pleural spines, and the presence of pygidial spines have been used to help differentiate between families of ptychopariids (e.g., Robison 1988; Ludvigsen et al. 1989) and corynexochids (e.g., Chang et al. 1980; Whittington 1995). Further investigations may determine if these character changes are the result of homeotic evolution and if homeotic evolution was in part responsible for some Cambrian supergeneric taxa.

Jacobs (1990) suggested that homeotic changes played an important role in the evolution of Bilateria in the early Phanerozoic. His work predicts that homeotic evolution should have been more frequent in the early evolution of arthropods because of the relative simplicity of gene regulation and the close spacing of Hox genes on the chromosome. This work provides a framework to test Jacobs's (1990) hypothesis. Homeotic change is present in the evolution of Cambrian trilobites, and this study suggests that it may be widespread. Further work on both Cambrian and post-Cambrian trilobites would help determine if homeotic evolution was more important in the early Paleozoic than in later times. Do post-Cambrian trilobites display homeotic evolution as often as Cambrian trilobites? Do Early Cambrian trilobites display more homeotic evolution than Middle or Late Cambrian trilobites?

Summary and Conclusions

Eight Hox genes are plesiomorphic to onychophorans and arthropods; thus, trilobites probably had all eight Hox genes. The trilobite Bauplan displays patterns of segment types that are consistent with the idea that trilobite segment morphology was controlled by Hox genes. These Bauplan patterns are used to define eight regions, which are identified here by the axial and pleural areas. These are the (1) frontal lobe (2) glabellar, (3) occipital ring, (4) anterior thoracic, (5) posterior thoracic, (6) articulating ring, (7) axial, and (8) terminal piece regions. The occipital ring and the articulating ring regions are transitional in morphology between the adjacent thoracic and either the glabellar or axial regions.

Unique characters are used to document several instances of homeotic evolution within Cambrian trilobites. In the oryctocephalids, homeotic evolution is widespread, as determined by the distribution of transglabellar furrows, lateral glabellar furrows, glabellar depressions, and pleural spines. A brief survey also indicates that Cambrian ptychopariids, redlichiids, and other corynexochids also display homeotic evolution with the redistribution of pleural spines and axial nodes.

Homeotic evolution is common in Cambrian trilobites, at least on the specific and generic levels, and may have had a hand in the evolution of supergeneric taxa. This work also suggests that paleontologists should explore the potential of homeotic evolution for other taxonomic groups.

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