

The Importance of Developmental Repatterning in the Evolution of Trilobites

Kenneth J McNamara

Department of Earth Sciences, University of Cambridge,
Downing Street, Cambridge CB2 3EQ, UK
✉ kjm47@cam.ac.uk

Manuscript received February 2010; accepted March 2010

Abstract

Historically, in his *On the Origin of Species*, Charles Darwin is remembered for, among other things, remarking on how poor the fossil record was and being concerned that it would not support his view of modification by natural selection. He is much less well remembered, though, for arguing for the importance of developmental change in inducing both intra- and interspecific variation. In this paper I explore how, using trilobites, the fossil record can be shown to reflect not only the patterns, but also the processes of evolution, in particular the important role of developmental repatterning (by heterochrony) in evolution. Examples are discussed from Early Cambrian oryctocephalid trilobites from China, and Late Devonian trilobites from Western Australia. Both show evolutionary trends fuelled by heterochrony. Although the targets of selection show significant differences between the Cambrian and Devonian, reflecting, perhaps, changes in the nature of the selection pressure, both demonstrate the importance of heterochrony in convergent evolution.

Keywords: development, evolution, heterochrony, trilobites, Cambrian, Devonian.

Introduction

“Geology assuredly does not reveal any such finely-graduated organic chain; and this, perhaps, is the most obvious objection which can be urged against this theory. The explanation lies...in the extreme imperfection of the fossil record.” (Darwin 1859, p. 280).

Of all the doubts expressed by Darwin about the validity of his theory of the origin of species by natural selection, it was the fossil record that seems to have given him the most sleepless nights. At such a nascent age in the development of geology as a science, it is really not surprising that Darwin’s opinion of the extent of palaeontological collections was less than enthusiastic: “...our richest geological museums ...what a paltry display we behold!” (Darwin 1859, p. 287). But with the burgeoning collections made, especially during the latter part of the 19th century, and into the succeeding centuries, not only have many examples of the finest gradations that Darwin expected to see been found in many taxa, but so too many of the so-called “missing links” between higher taxa, such as between fish and tetrapods and between dinosaurs and birds.

With the exploration of evolutionary transitions in the fossil record, from intraspecific to supraspecific levels, not only have the patterns of evolution been revealed, but so too have some of the mechanisms responsible for these changes (e.g. McNamara 1990). Foremost among this research has been the extent to which developmental change has played a primary role in evolution. Despite

being an unfashionable discipline in the late 1970s and early 1980s, a number of studies of the fossil record demonstrated that many of the phenotypic changes that occurred in many lineages could be explained by changes to developmental regulation – developmental repatterning (Arthur in press) (see McNamara 1997 for a review). The model used to interpret developmental changes in these palaeontological studies has been heterochrony. This is defined as changes to the rate and timing of developmental events, relative to the same events in the ancestor (Alberch *et al.* 1979; McKinney & McNamara 1991). Since these early works, much has been written on the role of heterochrony in evolution. To some, it is a major player in evolution (McKinney & McNamara 1991; McNamara 1995, 1997). Others have ascribed a more limited role Zelditch (2001) arguing that other processes, such as, ‘heterotopy’ (changing position) and ‘heterometry’ (changing number) are as important. This paper is not the appropriate vehicle to discuss the merits of these concepts, apart from making the point that changing position (heterotopy), changing number of meristic features (heterometry) both derive from changes to the timing and rate of developmental change. Thus it could be argued that they are mere subsets of heterochrony.

It is clear even from such a brief discussion as this that the study of developmental repatterning in evolution has been forever beset by questions of semantics. One of the delights of reading Darwin’s *On the Origin of Species* is the fact that he eschewed semantics. However, one consequence of this has been that many of his insights have often been under appreciated. Such is the case with his views on the role of development and embryology in evolution. Because so much of his book centres on the role of natural selection, and thus the extrinsic factors

driving evolutionary change, his thoughts on the intrinsic factors that contributed to the intraspecific phenotypic variation upon which natural selection works, have been rather neglected. Yet, reading the section on development and embryology, tucked away in the latter part of the 'Origin' reveals the importance with which Darwin viewed the role of developmental change in evolution. Moreover, it is then not too difficult to realise that many of the subsequent apparent breakthroughs, by workers such as Ernst Haeckel in the late nineteenth century and Walter Garstang and Gavin de Beer in the 20th century, had been anticipated by Darwin.

With the burgeoning interest in the relationship between developmental repatterning and evolution since the 1990s, often termed 'evolutionary developmental biology', or its less than euphonious epithet 'evo-dev', heterochrony has, to some degree, been reduced to something of a bit-player. While there are still many contemporary studies of heterochrony being carried out, (e.g., de Jong *et al.* 2009; Shitsukawa *et al.* 2009; Bertram *et al.* 2009) there are fewer examining its role in the fossil record. Is this because the importance of heterochrony is self evident? Or is it due to the problem of ascribing timing data to fossil material, making evaluation of heterochronic processes difficult? Or is just a casualty of changing scientific fashions? Here I wish to reiterate the importance of heterochrony in palaeontological studies and stress its usefulness as a model to explain phenotypic changes that have occurred in extinct organisms, using trilobites as the example.

Heterochrony encompasses both 'increase' and 'decrease' in the extent of developmental change between ancestors and descendants, depending on whether the descendant adult has gone through 'more' or 'less' developmental change than the ancestor (McKinney & McNamara 1991; McNamara 1993, 1997). If it has passed through more change it is known as *peramorphosis* (analogous to Haeckel's 'recapitulation'). Using the nomenclature of Alberch *et al.* (1979), this can occur by an increase in rate of development (*acceleration*); or by a delay in the offset of pre-adult growth (*hypermorphosis*) or by an earlier onset of growth of a particular trait (*pre displacement*). Correspondingly, if the descendant adult has passed through less developmental change than its ancestor, this is called *paedomorphosis*. This can occur by a reduction in the rate of growth (*neoteny* or *deceleration*); earlier offset of growth (*progenesis*) or a delay in the onset of growth of a trait (*post displacement*).

While the heritage of peramorphosis (under the guise of 'recapitulation') is generally traced back to the late 19th century and the work of Haeckel in the 1860s, and paedomorphosis to the work of Garstang in the 1920s, Darwin (1872, p. 395) had appreciated that both types of developmental repatterning played an important role in evolution by natural selection: "...it is highly probable that with many animals the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state."

On paedomorphosis acting intraspecifically, Darwin (1872, p. 395) observed: "With some animals the successive variations may have supervened at a very early period of life, or the steps may have been inherited at an earlier age than that at which they first occurred. In

either of these cases, the young or embryo will closely resemble the mature parent form..."

Whereas interspecifically (Darwin 1861, p. 393) he noted: "...some animals are capable of reproducing at a very early age, before they have acquired their perfect characters; and if this power became thoroughly well developed in a species, it seems probable that the adult stage of development would sooner or later be lost; and in this case, especially if the larva differed much from the mature form, the character of the species would be greatly changed and degraded."

In this paper I review heterochrony in trilobites separated by 150 million years: one of the earliest metazoans, Early Cambrian oryctocephalid corynexochid trilobites, and some of the last of their clades: Late Devonian trilobites comprising the last corynexochids, as well as the last harpetids, the last odontopleurids, phacopids and proetids. In addition to describing heterochronic repatterning in these groups, I will argue for the importance of heterochrony in generating evolutionary trends, and attempt to interpret the functional significance of some of the morphological changes engendered by heterochrony.

Trilobite Ontogenetic Development

Amongst arthropods, trilobites have a unique developmental system. The axis of the exoskeleton of adult trilobites is divided into the cephalon, thorax, and pygidium. The degree of segmentation expressed in these three regions is variable. It is most striking in the thorax, where the segments were articulated. The posterior of the cephalon and anterior of the pygidium each articulated with the anterior-most and posterior-most thoracic segments, respectively. Segmentation is also strongly expressed in the pygidium. However, the pygidial segments did not articulate as they were fused to one another. However, thoracic and pygidial segments had a common developmental origin. New post-cephalic segments were generated during ontogeny. The number of segments generated and their allocation to the thorax or pygidium varied ontogenetically and between taxa. As Hughes (2007) has pointed out, the post-cephalic region was either homonomous, where post-cephalic segments differed only in relative size or articulation pattern, or heteronomous, where the post-cephalic region possessed more than one type of segment.

As with other arthropods, trilobite development occurred through a series of instars, each produced by a moulting event. All trilobites may show a hemianamorphic pattern of development (Hughes *et al.* 2006) where the instars are typified initially by the sequential appearance of additional post-cephalic segments, followed by a sequence of instars with a fixed number of segments. This is known as the epimorphic phase (Hughes *et al.* 2006). New segments were formed adjacent to the anterior of the last segment of the post-cephalic region (Stubblefield 1926). Trilobite development is divided into three phases: the protaspid, meraspid and holaspid stages. The protaspid stage is characterized by the formation of facial sutures. The meraspid stage is marked by the separation of the cephalon and the post-cephalic region. During this period segments were

sequentially added at the front of the meraspid pygidium. The onset of the holaspid stage is characterised by the cessation of addition of segments to the thorax. During the meraspid period of segment addition, the number of segments in the pygidium could either decrease, stay fixed, or increase.

Heterochrony in Early Cambrian Oryctocephalid Trilobites from China

One of the striking features of the oryctocephalid trilobites that occur in the Early Cambrian Balang Formation in eastern Guizhou Province, southwest China, is the occurrence of convergent evolution in two clades of trilobites: in species of *Arthricocephalus* (McNamara *et al.* 2003) and in the *Duyunaspis-Balangia* clade (McNamara *et al.* 2006). Moreover the same morphological changes, that arise from developmental changes, and which are seen here at the specific and generic levels, have their parallels at the suprageneric level within oryctocephalid trilobites (McNamara 1986). Within a sequence of about 100m of shales of the Balang Formation, four species of *Arthricocephalus* occur. The oldest, and longest ranging, is *A. chaeveaui*, followed by *A. xinzhaiheensis*, *A. balangensis*, and lastly *A. pulchellus*. What most distinguishes these species is the number of thoracic and pygidial segments. All species possess 13 post-cephalic segments in the holaspid period. Whereas in *A. chaeveaui* there are 9 thoracic segments and 4 pygidial segments, in *A. xinzhaiheensis* there are 8 thoracic segments and 5 pygidial segments; in *A. balangensis* 7 thoracic segments and 6 pygidial segments, and lastly, with 6 thoracic segments and 7 pygidial segments, *A. pulchellus* (Figure 1). What is changing between these species is the location of the

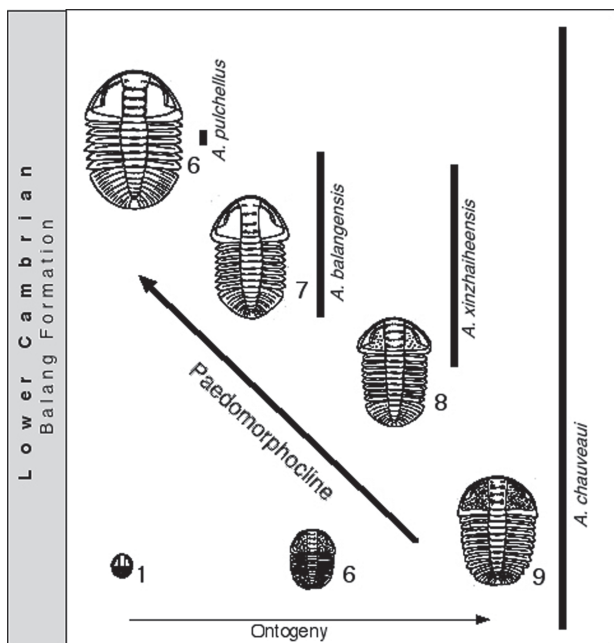


Figure 1. Pedomorphic evolution of species of the oryctocephalid trilobite *Arthricocephalus* from the Early Cambrian of Guizhou Province, China (after McNamara *et al.* 2003, text-Figure 8).

thoracic/pygidial margin. There is no evolutionary change in the extent of somitogenesis, *i.e.*, the rate of production of segments during ontogeny, but the difference is in the tagmosis, *i.e.*, the apportionment of segments between the thorax and pygidium. Thus each successively evolving species is pedomorphic relative to the presumed ancestor, the sequence of increasingly pedomorphic species forming a pedomorphocline (*sensu* McNamara 1982).

By investigating the ontogenetic development of segmentation in the oldest species, *O. chaeveaui*, it is possible to explain the developmental changes that are occurring between the four species. The ontogeny of the species can be subdivided into three phases. The first phase comprises meraspid stages 0–3; the second phase is meraspid stages 3 to 5; the third phase meraspid stages 5 to 9 (McNamara *et al.* 2006, text-Figure 9). The meraspid stage number relates to the number of thoracic segments present in that meraspid stage. In the first phase, between meraspids 0 to 3, 2 segments are added at each moult, but the thorax only increases by one. This means that the pygidium increases rapidly in number of segments, from 4 in meraspid 0 to 7 in meraspid 3. In the second ontogenetic phase somitogenesis ceases even though the trilobite is only partially through its meraspid period of development. The boundary between the thorax and pygidium migrates posteriorly, with the result that as the number of thoracic segments increases, the number of pygidial segments decrease. So by meraspid stage 5 there are 5 thoracic segments, but only 5 pygidial segments. In the final phase of meraspid development there is another growth pattern. Somitogenesis recommences so that at each moult an extra segment is added, the post-cephalic segment number increases from 10 to 13, and as it does so the boundary between the thorax and pygidium migrates posteriorly. So between meraspid stages 5 and 8 the pygidium always has 5 segments. Between the last two meraspid stages, 8 and 9, there is no new segment added, just the posterior movement of the boundary to reduce the pygidial segment number by one, to 4, and increase the thoracic segment number to its adult complement of 9.

The succeeding species, *A. xinzhaiheensis* reveals subtle differences in growth pattern, with one fewer post-cephalic segment at meraspid stage 3, but one more than *A. chaeveaui* in meraspid stage 5. The holaspid phase occurs when 8 thoracic segments have been produced, and the pygidium has 5 segments, a condition that is the same as meraspid stage 8 of the earlier, presumed ancestral species, *A. chaeveaui*. In this regard *A. xinzhaiheensis* can be regarded as pedomorphic. Only the last three meraspid stages of *A. balangensis* (meraspid stages 5 to 7) are known, and all have 13 post-cephalic segments, suggesting an acceleration in somitogenesis. The older *A. chaeveaui* at meraspid stage 5 had only produced 10 post-cephalic segments. However, cessation of somitogenesis occurred at an earlier stage in this descendant species. In the youngest species, *A. pulchellus*, only meraspid stage 6 was reached, before onset of maturity and cessation of production of new segments (Figure 1). In addition to changes in segment number the position of the fulcrum on the thoracic pleura changes from being set close to the distal margin in earlier

species, progressively moving in towards the axis in later species. This had the effect of increasing the overall convexity of the exoskeleton. Lastly, there were also pedomorphic changes to the cephalon, with a widening of the cephalon in later species; narrowing of fixigenae, deepening of glabellar furrows; and widening of the glabella.

The other oryctocephalid clade that occurs in the Balang Formation consists of two species, *Duyunaspis duyunensis* and *Balangia balangensis*. The heterochronic changes between the older *Duyunaspis* and younger *Balangia* mirror very closely the changes seen in the *Arthrocephalus* clade. When compared with *Balangia*, the holaspis of the older *Duyunaspis* has a greater number of thoracic segments (7) than *Balangia* (4). However, the pygidium of the holaspis of *Balangia* has the greatest number of segments (7), compared with *Duyunaspis* (5) (Figure 2). The holaspis of *Balangia* compares with the mid-meraspids of *Duyunaspis* in retaining a relatively narrow pygidium, the width being about two-thirds the length (McNamara *et al.* 2006). The holaspis of *Balangia* has free cheeks similar in width to those of a meraspis degree 4 of *Duyunaspis*. Like meraspids of *Duyunaspis*, the eye lobe is relatively longer in the holaspis of *Balangia*, compared with the holaspis of *Duyunaspis*.

The question has to be asked: what is the strong selection pressure on reducing thoracic segment number and increasing pygidial segment number and length in these two oryctocephalid clades? The answer probably lies in the inward movement of the fulcrum. The morphological consequence of this was that through both clades the overall convexity of the trilobites increased. By raising the level of the axis higher off the substrate, unless the trilobites underwent a lengthening of the pygidium, the posterior of the trilobite would be more exposed to predation. A lengthening of the pygidium to accommodate this was accompanied by a compensatory reduction in the number of thoracic segments. Selection pressure on increased height probably relates to increased predation pressure. Raising the exoskeleton

meant that the level of the eyes was raised, so increasing the range of vision (McNamara *et al.* 2006).

The reduction in number of thoracic segments seen in both oryctocephalid clades did not simply arise from neoteny or progenesis. In the *Duyunaspis*-*Balangia* clade, as thoracic segment number decreased along the clade, as occurred in *Arthrocephalus*, the number of pygidial segments increased: there was a developmental trade-off (*sensu* McNamara 1997). Two different mechanisms, somitogenesis and tagmosis, occurred during the ontogenetic development of the postcephalic region, and the rate and timing of change of these mechanisms appears to have varied independently, producing the heterochronic changes in the post-cephalic region in these two clades. Developmentally, it is more appropriate to consider the boundary between the thorax and the pygidium as migrating posteriorly at each moulting event, rather than the anterior-most pygidial segment moving anteriorly into the thorax. The mechanism for these changes is described in detail in McNamara *et al.* (2003, 2006).

Heterochrony in Late Devonian Trilobites from Western Australia

For a length of about 350 km Late Devonian sedimentary rocks are present along the south-western margin of the Kimberley Block in the northern Canning Basin in Western Australia. These rocks are the remains of a major reef complex that existed during the late Givetian to Famennian. Within the marginal slope facies, known as the Virgin Hills Formation, trilobites occur. The oldest part of the Virgin Hills Formation to yield trilobites is Frasnian conodont Zone 11 in age (Klapper 2007). They occur commonly through Zones 12 and 13b, and into the overlying Famennian to the *rhomboidea* Zone. The Frasnian-Famennian boundary represents one of the major Phanerozoic mass extinction events and greatly impacted trilobite biodiversity.

Five orders of trilobites are present in the Virgin Hills Formation: Corynexochida (McNamara & Feist 2006); Odontopleurida (Feist & McNamara 2007), Harpetida (McNamara *et al.* 2009), Phacopida (Feist *et al.* 2009) and Proetida (McNamara & Feist 2008). The first three orders became extinct globally at the end of the Frasnian Stage, their representatives surviving in the Virgin Hills Formation to the last zone of the stage. Evolutionary changes in all groups, either before or after the Frasnian/Famennian boundary, show varying degrees of heterochrony. Where suitable ontogenetic information is available, the role of developmental repatterning in response to changing environmental conditions can be determined. Of particular interest are variations in eye morphology prior to and after the Frasnian/Famennian boundary in a number of clades within the Corynexochida, Phacopida and Proetida. Although some species are blind, others show evolutionary trends of varying numbers of lenses arising from heterochronic changes.

Corynexochida

The last surviving family of the Corynexochida is the Scutelluidae. This family is represented in the Frasnian

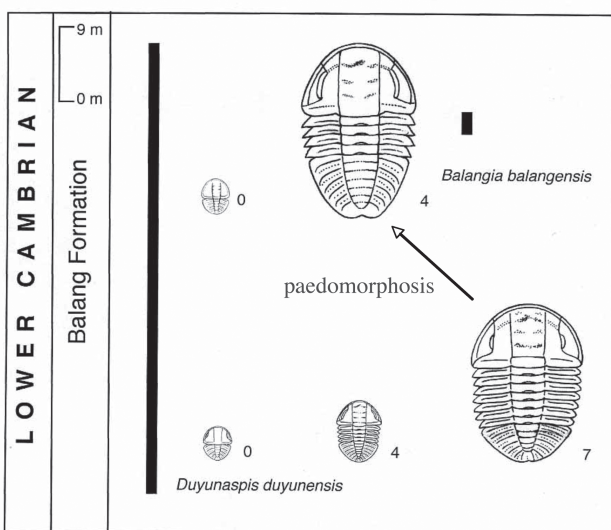


Figure 2. Paedomorphic evolution of species of the oryctocephalid trilobites *Duyunaspis* and *Balangia* from the Early Cambrian of Guizhou Province, China (after McNamara *et al.* 2006, text-Figure 8).

of the northern Canning Basin region by the last two known species of the order, *Telopeltis woodwardi* McNamara & Feist 2006, which ranges from Zones 11 to 12, and *T. microphthalmus* McNamara & Feist 2006, from Zones 13a and 13b. *Telopeltis* is an unusual scutelluid in possessing a very convex exoskeleton, the pygidium being especially strongly convex. However, there is a reduction in convexity between the two species. A trend of reduced convexity also occurs in other trilobite groups in the Virgin Hills Formation (see below). Moreover, the eye lobe reduces in size in the younger species of *Telopeltis* (Figure 3). Eye reduction also occurs in other trilobite groups in the Frasnian part of the Virgin Hills Formation.

A strongly vaulted transitory pygidium typifies early ontogenetic growth in many phylogenetically older scutelluids, the adults developing a much flatter pygidium. This suggests that in adults of *Telopeltis* this character is pedomorphic. A further five pedomorphic features are present in the younger species, *T. microphthalmus* and eight in *T. woodwardi*. These include glabellar furrow depth, development of occipital spine, in addition to the reduction in eye size, and higher exoskeletal vaulting (McNamara & Feist 2006, p. 990). The relatively small size of these species compared with

phylogenetically earlier scutelluid genera suggests that possibly the pedomorphic features evolved in response to selection for earlier maturation in a stressed environment (McNamara & Feist 2008, p. 270).

Odontopleurida

These are rare trilobites in the Virgin Hills Formation of the fauna. Species present in zone 13b of the latest Frasnian are the last representatives of the order Odontopleurida and belong in the family Odontopleuridae. Five species are known from zones 11 to 13b and all are placed within the genus *Gondwanaspis* (Feist & McNamara 2007). Only two of the Kimberley species have been formally named: *G. spinosa* Feist & McNamara, 2007 and *G. dracula* Feist & McNamara, 2007, due to paucity of material of the other taxa. *Gondwanaspis* is typified by a very low convexity, wide cephalon, poorly defined glabellar lobes and presence of spines or protuberances on the anterior margin of the cranidium. Feist & McNamara (2007) have suggested that the absence of an anterior cephalic arch seen in other odontopleurids is because of a downward flexure of the anterior margin. As a result *Gondwanaspis*, unlike other odontopleurids, instead of having to assume both a 'resting' and an 'active' posture, could assume a single

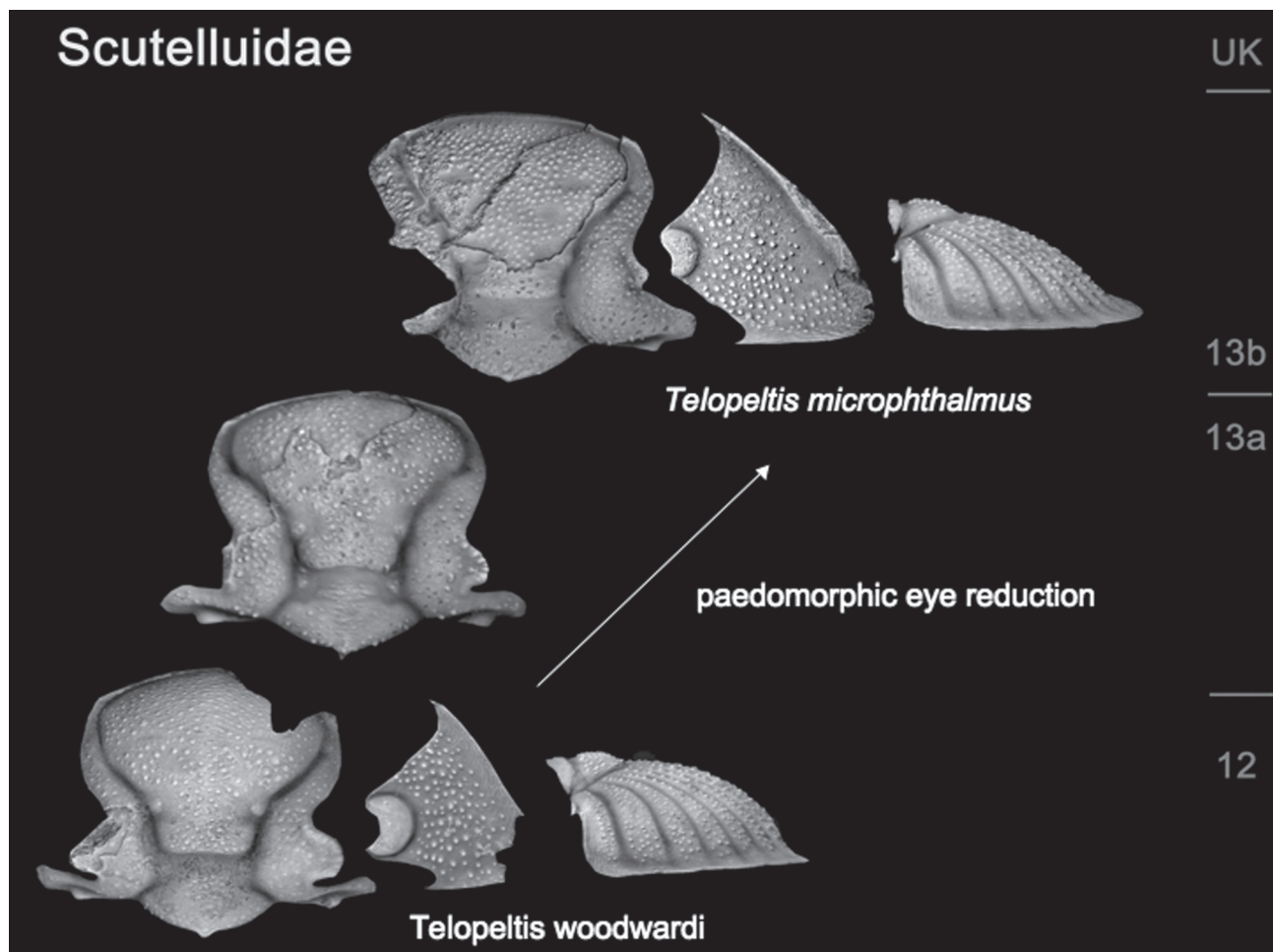


Figure 3. Evolution in species of the scutelluid trilobite *Telopeltis* from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.

posture. The effect of this, along with the low convex cephalon and wide genal areas, was that the eye would have been positioned laterally, so as to reduce a potential appreciable anterior blind spot.

Consistent ontogenetic changes occur in a wide range of odontopleurids. These suggest that in *Gondwanaspis* some of the cephalic features evolved by paedomorphosis. These include the poorly developed glabellar lobes, the frequent anterior position of the eye lobe, and the truncate frontal lobe (Feist & McNamara 2007).

Harpetida

Harpetid trilobites are particularly common in the Frasnian part of the Virgin Hills Formation (McNamara *et al.* 2009). Two genera have been described. Of these, *Eskoharpes* is the most diverse and long-ranging, with four species that extend from Zones 11 to 13b. The type species, *E. palanasus*, is the last known member of the order Harpetida. Four species of *Eskoharpes* (Figure 4) show evolutionary trends in decreasing convexity of the cephalon and increase in the brim width. These changes have been attributed to heterochrony, and as such represent the first record of heterochrony in harpetid trilobites (McNamara *et al.* 2009, p. 28). Reasonably complete ontogenies of the last species of *Eskoharpes*, *E.*

palanasus (Zones 13a–b), and of the earliest species, *E. wandjina* (Zones 11–12), has enabled the role that heterochrony played in the evolution of *Eskoharpes* to be determined.

The morphological changes that occurred in the cephalon of *E. wandjina* during ontogeny between early meraspids and holaspids are not great. The early meraspid cephalon, like that of the holaspid, has a strongly vaulted glabella and genal areas. The brim undergoes little relative increase in width between meraspids and the large holaspids. In meraspids the genal roll (see McNamara *et al.* 2009, text-Figure 2) is a little narrower than in larger specimens, but it was steeply inclined in all growth stages. The phylogenetically younger *E. palanasus* underwent much greater morphological change during ontogeny. During the meraspid phase of growth the brim became relatively wider; the external rim relatively narrower; the glabella broader, but less inflated and less steeply inclined; the genal areas less swollen; the genal roll more shallowly inclined; axial and posterior furrows less incised; and the alar furrows more pronounced (Figure 4).

The meraspid cephalons of this last species of *Eskoharpes* resemble both the meraspid and holaspid cephalons of the earlier species, *E. wandjina* and *E. boltoni* (Zone 12). The fact that *E. palanasus* underwent a greater degree of

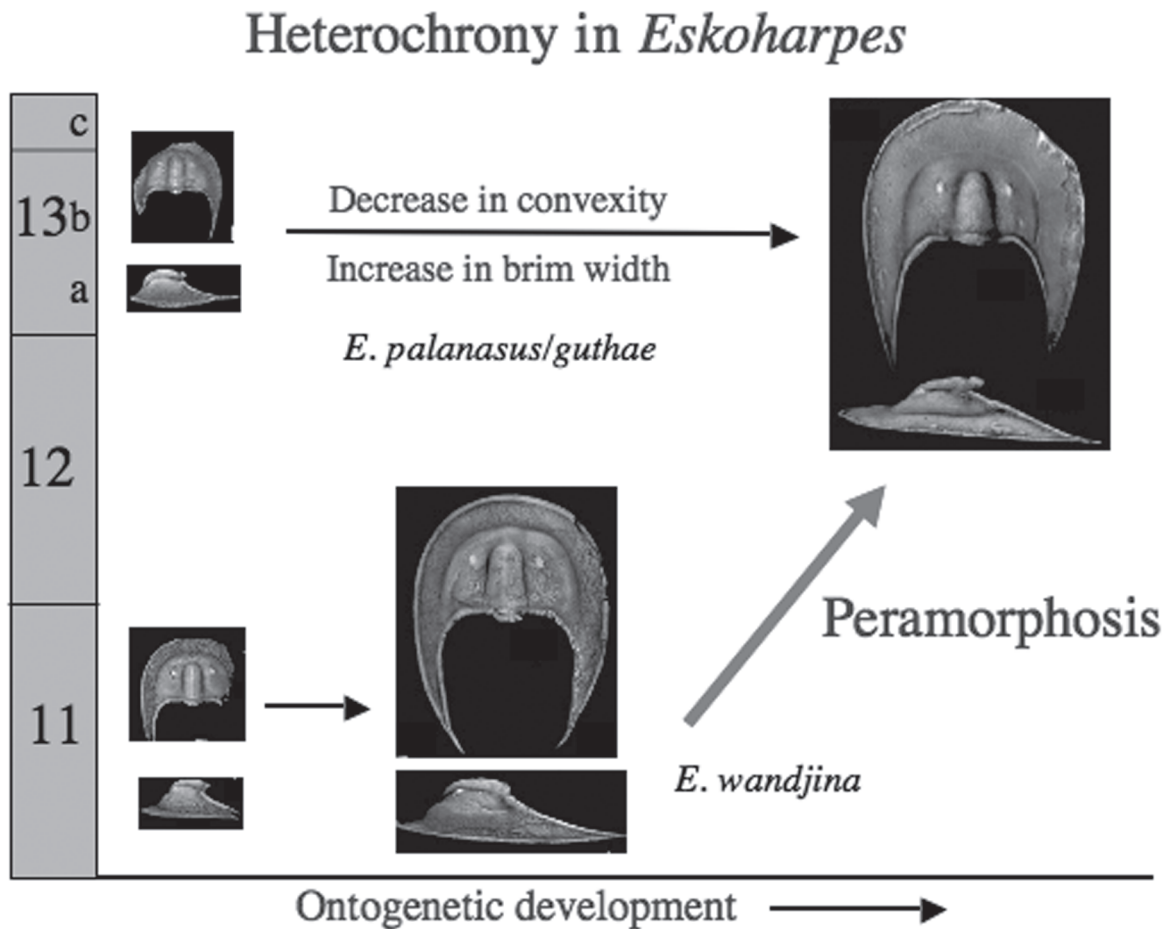


Figure 4. Peramorphic evolution in species of the harpetid trilobite *Eskoharpes* from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia (after McNamara *et al.* 2009, text-Figure 5).

morphological change during ontogeny than earlier species, indicates evolution by peramorphosis. The phylogenetically younger species do not attain the same size as the earliest species, *E. wandjina*, but compare in size to the Zone 12 species, *E. boltoni*. Although actual growth rates are not known, the greater morphological development in the younger species might have arisen from an acceleration in growth rates. The main morphological features that can be described as peramorphic are brim width, and genal roll, glabella and genal vaulting. This represents the first record of peramorphosis in Devonian trilobites (McNamara *et al.* 2009).

Phacopida

The phacopid *Acuticryphops acuticeps* (Kayser 1889) became increasingly common prior to the Frasnian/Famennian mass extinction event (Feist *et al.* 2009). A pedomorphic reduction in eye lens number has been documented in *A. acuticeps* which occurs not only in the fore-reef facies of the Late Devonian reefs of Western Australia, but also in a number of locations worldwide, such as Montagne Noire and Morocco (Feist 1995; Crônier *et al.* 2004; Feist *et al.* 2009). In the material from the Montagne Noire and Morocco eye reduction occurred intraspecifically. However, in the Virgin Hills Formation

the pedomorphic reduction occurred between two species, *A. acuticeps* from Zone 13a and *A. klapperi* Feist *et al.* 2009 from Zone 13b (Figure 5). *A. acuticeps* has between 6 and 13 lenses in each eye. In *A. klapperi* it was reduced to between 3 and 6 lenses.

Six species of early Famennian phacopids have been described from the Virgin Hills Formation (Feist *et al.* 2009). Phacopids have not been found immediately after the mass extinction event. The first occurrence is in the middle *triangularis* zone. In Europe only blind phacopids are known in the earliest Famennian. However in the Canning Basin reef environment initial recovery following the mass extinction involved oculated forms, notably species of *Houseops*. The three species of this genus, described by Feist *et al.* (2009), *H. canningensis*, *H. beckeri* and *H. sp. A*, are thought to have evolved from conservative oculated ancestors that had survived the end Frasnian biocrises in reefal shallow water niches. Unlike the trends in eye reduction that occur in *Acuticryphops* in the latest Frasnian, descendant lineages in the Famennian show increasing number of lenses in the eye, increased cephalic vaulting and effacement. The earliest form of *Houseops*, *H. sp.* had 25 lenses per eye, *A. beckeri* 48 lenses, and the youngest species *A. canningensis* 59. Given that the cephalata of all three species are of a similar size, then it can be presumed that

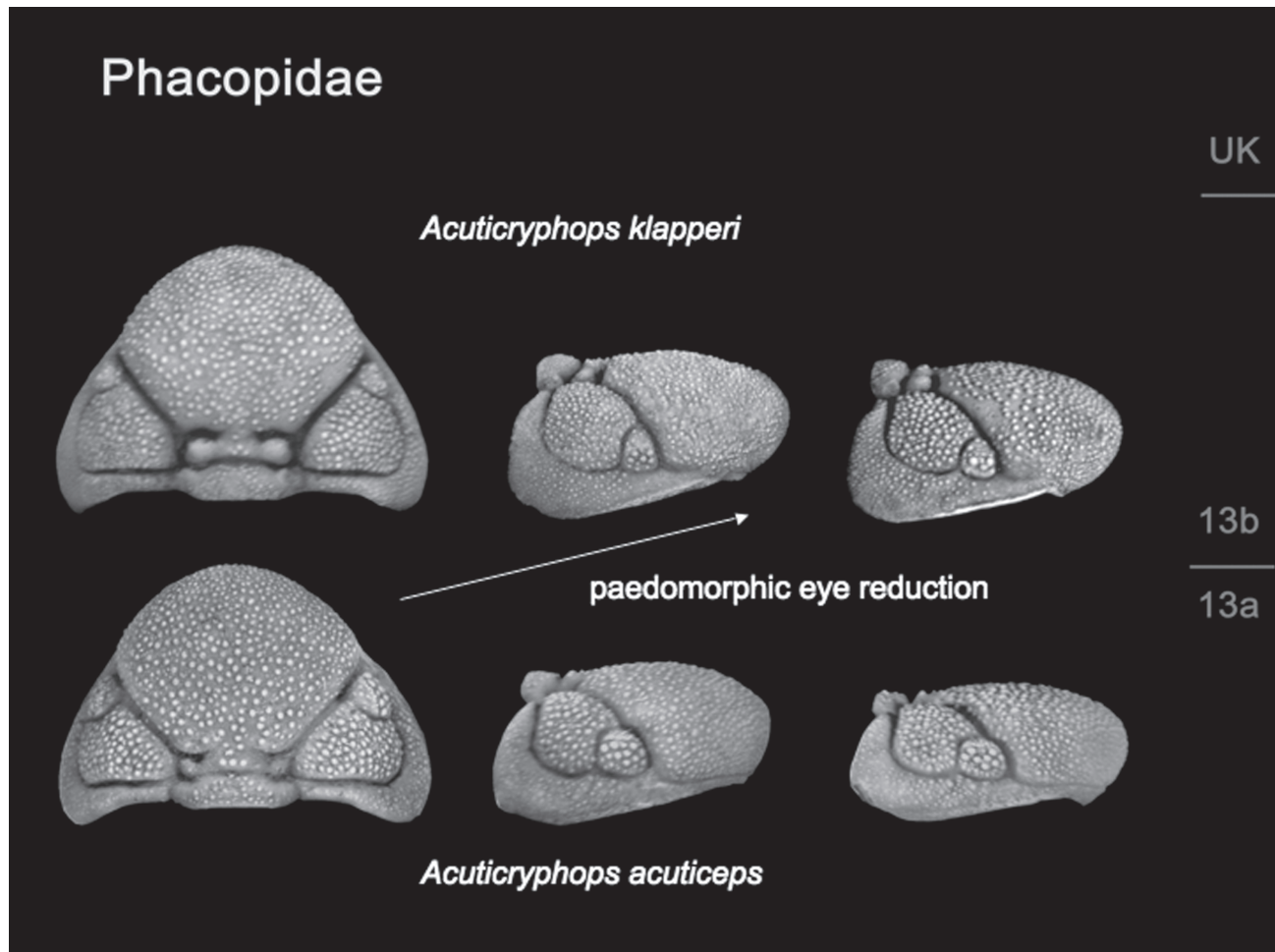


Figure 5. Paedomorphic eye reduction in species of the phacopid trilobite *Acuticryphops* from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.

the increase in lens number is a peramorphic trait, either by acceleration, or predisplacement.

Proetida

The most abundant trilobite order found in the Virgin Hills Formation is the Proetida, with three genera and 15 species (Feist & McNamara in prep.). Evolutionary trends occur in a number of clades, with changes affecting, in particular, the eyes. In an undescribed drevermaniine genus large eyes and palpebral lobes are present in species between Zones 11 and Zone 13b. However the three species that occur in this genus show a progressive, albeit small, paedomorphic decrease in eye size (Figure 6). From these oculated proetids evolved the *Palpebralia* lineage. This had a worldwide distribution in off-shore or deeper ramp environments (McNamara & Feist 2008). *Palpebralia* underwent evolutionary trends in eye-reduction and straightening of the palpebral suture. In the Virgin Hills Formation five different morphs of *P. palpebralis* with a variable degree of regression of the palpebral lobe can be distinguished with four taxa of *Palpebralia* being blind (McNamara & Feist 2008). The eye reduction in the undescribed drevermaniine and in *Palpebralia* both occurred by paedomorphic reduction in size and in number of lenses in the eye. Another proetid,

the blind *Pteroparia*, is an extreme paedomorphic form which displays an extreme backward migration of the facial suture, extending this trend that is a feature of the *Pteroparia* evolutionary lineage elsewhere (Feist & Clarkson 1989).

Discussion

During the late Frasnian, evolutionary trends in scutelluid, phacopid and a number of proetid lineages involved, among others, a reduction in eye lens number and diminution in size of the eye in a number of unrelated lineages. These reductions were induced by the operation of paedomorphic processes and show that heterochrony is a significant factor in convergent evolution. McNamara (1986) argued that paedomorphosis was the dominant form of heterochrony in Cambrian trilobites. It appears to have likewise been more common than peramorphosis in the late Devonian trilobites discussed here, although some of the Devonian trilobites do also show evidence for peramorphic processes, in particular the development of the brim in harpetids and the increase in eye lens number in some phacopids during the early Famennian.

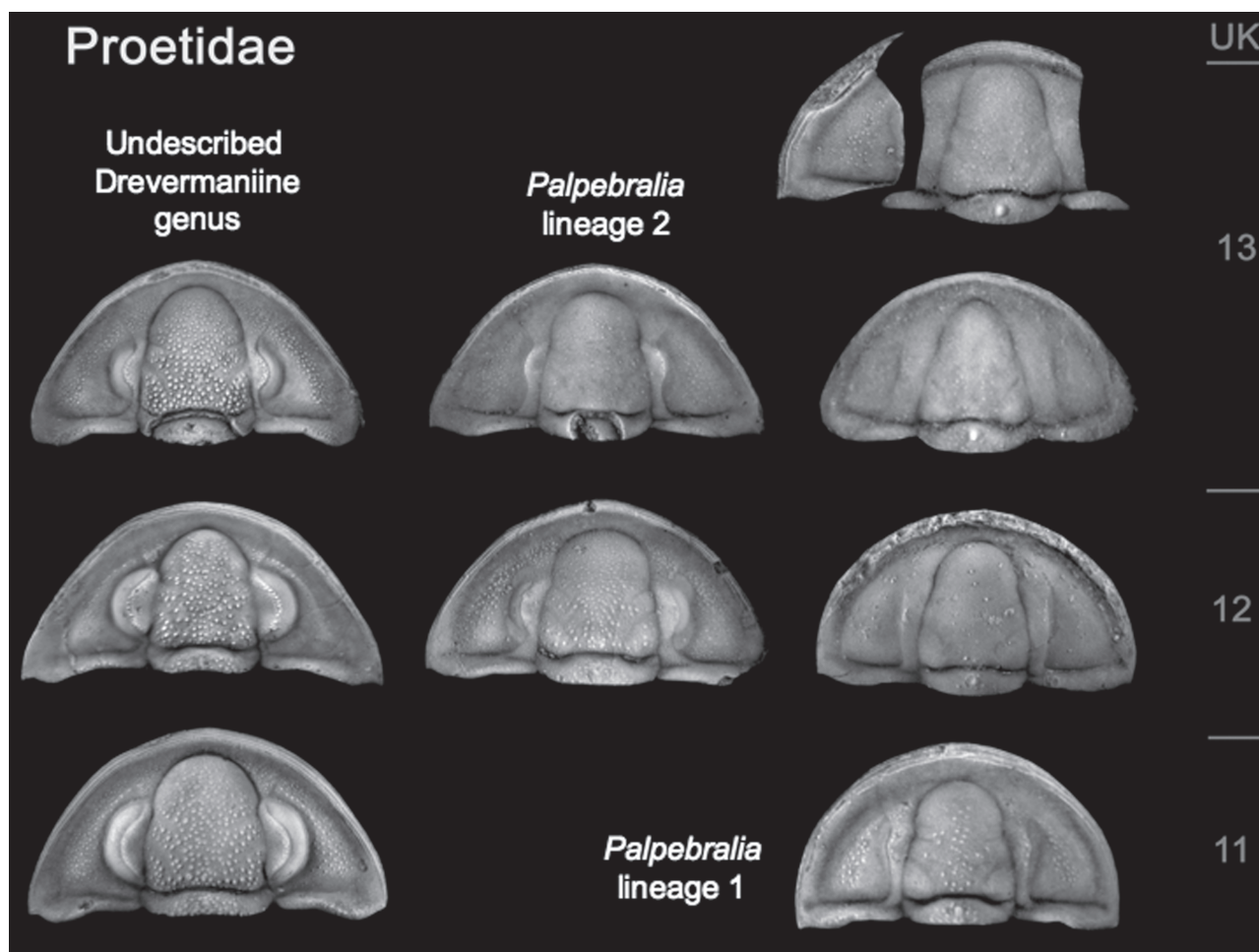


Figure 6. Paedomorphic eye reduction in three lineages of proetid trilobites from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.

The early Cambrian oryctocephalids also show a predominance of paedomorphosis. Although this had some effect on eye position it was more targeted on thoracic and pygidial segment number. The nature of the Devonian material is such that details of thoracic segment number are not known and so it is not possible to determine if heterochrony had any significant effect on the segment numbers generated during ontogeny. However, in groups such as the Phacopina segment number was fixed at 11 in all families. This reflects a post-Cambrian 'developmental hardening', as suggested by McNamara (1986), whereby there was a greater fluidity in thoracic segment number at lower taxonomic levels in the Cambrian compared with the post-Cambrian. Variation in segment number could even occur intraspecifically in some early Cambrian taxa, such as members of the Emuellidae (Paterson & Edgecombe 2006), this variation declining from the Middle Cambrian (Webster 2007). In the oryctocephalids it varied intraspecifically.

As well as the Cambrian and Devonian examples discussed here showing examples of convergent evolution in thoracic and pygidial segment number in Cambrian forms and eye size and lens number in Devonian taxa, both also show changes in exoskeletal convexity along lineages. In the case of the Cambrian oryctocephalids, this involved an increase in overall convexity. In the Devonian harpetids and scutelluids, this involved a decrease in cephalic convexity. While it has been argued that increasing convexity can confer a selective advantage to the trilobite in terms of improved visual capability (McNamara *et al.* 2003, 2006), there is no obvious selective advantage to reduced convexity, although one possibility is that it could have improved the ability of the trilobites to burrow in the sediment. Alternatively it could indicate that there had been a reduction in the selection pressure for improved vision. This could have been by a reduction in predation pressure during the lead up to the Frasnian/Famennian mass extinction event.

It has been suggested (Feist *et al.* 2009; McNamara & Feist 2008) that reduction in lens number in a number of scutelluid, phacopid and proetid lineages may reflect selection associated with global sea level rise in the late Devonian. This culminated in an increase in water depth immediately prior to the final extinction event, the so-called Upper Kellwasser extinction. Reappearance of oculated phacopids and peramorphic increase in lens number in the early Famennian correlates with a period of regression and thus shallowing of water in the marginal slope environment (Feist *et al.* 2009). Profound eustatic perturbations during the late Devonian may thus have played a significant role in determining which type of heterochrony prevailed.

Conclusions

In his attempts in *On the Origin of Species* to explain the nature of intraspecific variation, the raw material upon which natural selection operates, Darwin stressed the importance of changes to development. This surprisingly unheralded aspect of Darwin's work has been the subject of increased interest in recent years, where the role of developmental repatterning in

evolutionary change has been shown to have played a major role in evolution. Darwin was also concerned that what he perceived as the poor fossil record did little to support his model of natural selection. However, many studies, especially within the last 30 years, have shown that the fossil record is sufficiently extensive to be used to demonstrate not only the patterns of evolution, but also their processes. In particular developmental repatterning, in the form of heterochrony has been shown to have been significant in the evolution of many groups of vertebrates and invertebrates.

The nature of the pattern of development of trilobites, especially with the progressive decreases through ontogeny in the number of thoracic segments, has encouraged a relatively large number of studies of the effect of heterochrony on the evolution of the group. These have shown the overwhelming importance of paedomorphosis, with many Cambrian clades having experienced reductions in the number of thoracic segments through time. By contrast, studies of heterochrony in later Palaeozoic trilobites have demonstrated more the significance of allometric changes, such as to cephalic shape and to eye size. While these studies have illustrated the continuing importance of heterochrony in the evolution of these later trilobites, both paedomorphosis and peramorphosis have been shown to have played significant roles in evolutionary trends in many clades.

Acknowledgement: I am grateful to Raimund Feist, my collaborator on the research into the Late Devonian trilobites, for his insights, and for providing the photographs used in the figures.

References

- Alberch P, Gould S J, Oster G F & Wake D B 1979 Size and shape in ontogeny and phylogeny. *Paleobiology* 5: 296–317.
- Arthur W (in press) *Evolution – a Developmental Approach*. Wiley-Blackwell.
- Bertram D F, Phillips, N E & Strathmann R R 2009 Evolutionary and experimental change in egg volume, heterochrony of larval body and juvenile rudiment, and evolutionary reversibility in pluteus form. *Evolution & Development* 11: 728–739.
- Crônier C, Feist R & Auffray J-C 2004 Variation in the eye of *Acuticryphops* (Phacopina, Trilobita) and its evolutionary significance: a biometric and morphometric approach. *Paleobiology* 30: 471–81.
- Darwin C 1859 *The Origin of Species by Means of Natural Selection*. John Murray, London.
- Darwin C 1861 *The Origin of Species by Means of Natural Selection* (3rd ed). John Murray, London.
- Darwin C 1872 *The Origin of Species by Means of Natural Selection* (6th ed). John Murray, London.
- de Jong A U, Ilse M L, Colbert M W, Witte F & Richardson M K 2009 Polymorphism in developmental timing: intraspecific heterochrony in a Lake Victoria cichlid. *Evolution & Development* 11: 625–635.
- Feist R 1995 Effect of paedomorphosis in eye reduction on patterns of evolution in trilobites. In K J McNamara (ed) *Evolutionary Change and Heterochrony*. Wiley, Chichester, pp 225–244.
- Feist R & Clarkson E N K 1989 Environmentally controlled phyletic evolution, blindness and extinction in Late Devonian tropidocoryphine trilobites. *Lethaia* 22: 359–373.

- Feist R & McNamara K J 2007 Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetian, Frasnian). *Geological Magazine* 144: 777–796.
- Feist R, McNamara K J, Cronier C & Lerosey-Aubril R 2009 Patterns of extinction and recovery of phacopid trilobites during the Frasnian-Famennian (Late Devonian) mass extinction event, Canning Basin, Western Australia. *Geological Magazine* 146: 12–33.
- Hughes N C, Minelli A & Fusco G 2006 The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology* 32: 602–627.
- Hughes N C 2007 The evolution of trilobite body patterning. *Annual Review of Earth and Planetary Science* 35: 401–434.
- Klapper G 2007 Frasnian (Upper Devonian) conodont succession at Horse Spring and correlative sections, Canning Basin, Western Australia. *Journal of Paleontology* 81: 513–537.
- McKinney M L & McNamara K J 1991 *Heterochrony: the Evolution of Ontogeny*. Plenum, New York.
- McNamara K J 1982 Heterochrony and phylogenetic trends. *Paleobiology* 8: 130–142.
- McNamara K J 1986 The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews* 61: 121–156.
- McNamara K J (ed) 1990 *Evolutionary Trends*. Belhaven Press, London & University of Arizona, Tucson.
- McNamara K J 1993 Inside evolution. *Journal of the Royal Society of Western Australia* 75: 3–12.
- McNamara K J (ed) 1995 *Evolutionary Change and Heterochrony*. Wiley, Chichester.
- McNamara K J 1997 *Shapes of Time: the Evolution of Growth and Development*. The Johns Hopkins University Press, Baltimore.
- McNamara K J & Feist R 2006 New styginids from the Late Devonian of Western Australia – the last corynexochid trilobites. *Journal of Paleontology* 80: 981–992.
- McNamara K J & Feist R 2008 Patterns of trilobite evolution and extinction during the Frasnian/Famennian mass extinction event, Canning Basin, Western Australia. In I Rábano, R Gozalo & D García-Bellido (eds) *Advances in Trilobite Research*. Cuadernos del Museo Geominero, 9. Instituto Geológica de España, Madrid, pp 269–274.
- McNamara K J, Yu F & Zhou Z 2003 Ontogeny and heterochrony in the oryctocephalid trilobite *Arthricocephalus* from the Early Cambrian of China. *Special Papers in Palaeontology* 70: 103–126.
- McNamara K J, Yu F & Zhou Z 2006 Ontogeny and heterochrony in the oryctocephalid trilobites *Changaspis*, *Duyunaspis* and *Balangia* from the Lower Cambrian of China. *Palaeontology* 48: 1–19.
- McNamara K J, Feist R & Ebach M 2009 Patterns of evolution and extinction in the last harpetid trilobites during the Late Devonian (Frasnian). *Palaeontology* 52: 11–33.
- Paterson J R & Edgecombe G D 2006 The Early Cambrian trilobite family Emuellidae Pocock, 1970: systematic position and revision of Australian species. *Journal of Paleontology* 80: 496–513.
- Shitsukawa N, Kinjo H, Takumi S & Murai K 2009 Heterochronic development of the floret meristem determines grain number per spikelet in diploid, tetraploid and hexaploid wheats. *Annals of Botany* 104: 243–251.
- Stubblefield C J 1926 Notes on the development of a trilobite, *Shumardia pusilla* (Sars). *Zoological Journal of the Linnean Society*, London 35: 345–372.
- Webster M 2007 A Cambrian peak in morphological variation within trilobite species. *Science* 317: 499–502.
- Zelditch M L 2001 *Beyond Heterochrony*. Wiley, New York.