ANCIENT ANIMAL MIGRATION: A CASE STUDY OF EYELESS, DIMORPHIC DEVONIAN TRILOBITES FROM POLAND

by BŁAŻEJ BŁAŻEJOWSKI1, CARLTON E. BRETT2, ADRIAN KIN3,†, ANDRZEJ RADWAŃSKI4,† and MICHAł GRUSZCZYŃSKI3,†

1Institute of Palaeobiology, Polish Academy of Sciences, Twarda 51/55, 00-818, Warszawa, Poland; bblazej@twarda.pan.pl
2Department of Geology, University of Cincinnati, Cincinnati, OH 45221-0013, USA; brettce@ucmail.uc.edu
3'Phacops' – Association of Friends of Geosciences, Grajewska 13/40, Warszawa, 02-766, Poland
4Institute of Geology, University of Warsaw, Zwirki i Wigury 93, 02-089, Warszawa, Poland

Typescript received 15 February 2016; accepted in revised form 8 July 2016

Abstract: We report evidence of one of the oldest known animal migratory episodes in the form of queues of the eyeless trilobite *Trimerocephalus chopini* Kin & Błażejowski, from the Late Devonian (Famennian) of central Poland. In addition, there is evidence for two morphs in this population, one with nine segments and the other with ten. We infer that these queues represent mass migratory chains coordinated by chemotaxis, comparable to those observed in modern crustaceans such as spiny lobsters, and further suggest that the two forms, which occur in an approximately 1:1 ratio, may be dimorphs. These ancient arthropods may have migrated periodically to shallow marine areas for mass mating and spawning. The sudden death of the trilobites in the queues may have been caused by excess carbon dioxide and hydrogen sulphide introduced into the bottom water by distal storm disturbance of anoxic sediments. This study demonstrates the potential for further research on the evolution and ecology of aggregative behaviour in marine arthropods.

Key words: animal migration, eyeless trilobite, Phacopinae, Devonian, Holy Cross Mountains, Poland.

PERIODIC mass migrations have been observed in many modern groups of vertebrate and invertebrate animals (Hoare 2009a, b). There are several possible functions of such periodic migratory behaviour including reproductive and trophic aggregations (Thollot *et al*. 1999; Crossin *et al*. 2009). Recent studies on the processes controlling mass migrations (Wilcove 2008) form an important aspect of behavioural science, particularly migrations related to human activity and rapid variations of climates, but very little is yet known about the evolutionary origin and ecological significance of mass migrations, which have rarely been recognized in the fossil record. Chain-like clusters of the enigmatic early Cambrian arthropod (crustacean?) *Synophalos xynos* have been described before (Hou *et al*. 2008, 2009); in this example the organisms were seemingly linked in that the caudal region of each individual inserted into the anterior carapace of the one behind. The authors interpreted these chains as probable migratory aggregates. However, the forms and structures described are distinct from positions or behaviour known in trilobites, as briefly noted earlier (Radwański *et al*. 2009, p. 467). Linear clusters of trilobites are also known from the Ordovician of Morocco (Chatterton & Fortey 2008) and that of Portugal (Gutiérrez-Marco *et al*. 2009), but their relationship to migration or mating aggregation has not been pursued in detail. These instances in distantly related clades, however, may point to a more common phenomenon among arthropods than previously recognized.

New material from the Kowala Quarry (Holy Cross Mountains, Central Poland) described herein has great potential for the study of the nature of such migrations based on queues of the blind phacopide trilobite *Trimerocephalus*. A previous study of these queues (Radwański *et al*. 2009) concerned the structure (organization) of queues in relation to the interpreted ambient environment. Size frequency aspects and dimorphism, were not discussed in the former study. Thus, the present paper aims to provide substantial further details and discussion

†Deceased
of the significance of these findings and a reinterpretation of queues as evidence for migratory behaviour, probably in association with reproduction in these blind trilobites.

MATERIAL AND METHOD

All trilobites discussed herein occur in an approximately 25 m thick succession of marly shales in the early Famen- nian (approximately 365 Ma), at the Kowala Quarry near Kielce, Holy Cross Mountains, central Poland (Fig. 1) (Radwański et al. 2009). A total of 78 examples of rows or queues of the blind trilobite Trimerocephalus chopini Kin & Błażejowski, 2013, have been obtained, each with up to 19 aligned, articulated individuals. These trilobite queues are preserved within three horizons of marly shales with occasional small, calcareous concretions. Trilobites in the queues are arranged in the same direction, one after the other, in cephalon to pygidium (head to tail) manner, and frequently contact or overlap each other (Figs 2A, C; 3). All specimens are preserved in apparent life-positions and those in queues fall into a relatively narrow size range relative to those seen in other phacopine trilobites (7–19 mm in length). Nearly all specimens are fully articulated and a few individuals preserve elements of locomotory appendages (i.e. endo- and exopodites), indicating rapid, in situ burial. They are directly associated with numerous small enrolled specimens of T. chopini. One exceptionally preserved specimen, examined in detail using x-ray tomography, revealed the oldest fully preserved moulting episode (exuvium plus soft-shelled trilobite) known from the fossil record (Błażejowski et al. 2015).

All trilobite specimens have been prepared manually. The collected material is housed at the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw (ZPAL Tr.8).

Carbon dioxide for isotopic analysis of matrix carbonate was extracted either manually using traditional vacuum extraction lines or using an automated online Isocarb reaction system. Carbon and oxygen stable isotope data were obtained using a Finnigan MAT 251 mass spectrometer at the University of Liverpool. All isotopic data are reported with reference to the VPDB international standard; typical precisions of 0.1 ‰ are reported by this laboratory. Statistical calculations were performed with PAST v. 3.01 (Hammer et al. 2001).

RESULTS

The size-range of articulated trilobite exoskeletons within the queues varies somewhat. Surprisingly, however, the studied specimens in ten sample queues have an inconsistent number of thoracic segments, with nearly equal numbers of two morphs (Kin & Błażejowski 2013): 51% of individuals have nine segments, while 49% have ten

---

**FIG. 1.** A, map of Poland indicating the location of the Holy Cross Mountains area (HCM; rectangle). B, generalized geological map of the Holy Cross Mountains and the location of Kowala Quarry (arrowed). C, map of Kowala Quarry with the location of the studied section exposed in the western part of the northern quarry wall (arrowed). Scale bars represent 100 km (A); 10 km (B); and 0.5 km (C).
In general, the 9-segmented morphs are smaller ($N = 34$; mean = 8.8 mm; range: 5–12 mm) than 10-segmented forms ($N = 36$; mean = 14.5 mm; range: 7–19 mm); the medians are significantly different (Mann-Whitney U-test: $U = 90$; $p = 6.669$).

In addition, at least 119 enrolled specimens were found in association with the queues at each of the three levels, though typically a few millimetres above the bedding planes containing the queues. These specimens usually range in cephalic size from 2 to 4 mm.

Geochemical and mineralogical investigations revealed very fine-grained calcareous silt with abundant limonitic pseudomorphs after original pyrite, directly underneath individual $T. chopini$ skeletons from the trilobite queues. Carbonate sediment underneath the individual $T. chopini$ exuviae, yielded $\delta^{13}C$ values that oscillated around $-1.5\%$, whereas values for the sediment underneath the trilobite skeletons in the queues are somewhat higher, being around $-0.3\%$ PDB (Fig. 4G–H).

**DISCUSSION**

*Seasonal migrations of modern marine arthropods: a modern analogue*

Among modern marine arthropods, the phenomenon of mass seasonal migration has been observed, for example, among spiny lobsters (Decapoda, Palinuridae) in pre-adult, moulting and reproductive phases of their life cycle (Herrnkind 1980) (Fig. 2B). Reproductive cycles are the major causes of periodic mass migration in the spiny lobster $Panulirus argus$ (Linnaeus), similar to that photographed by Herrnkind (1975, p. 828), Bimini (Bahamas). Another example of $T. chopini$ queue (formed by over ten well-aligned specimens; Kow/Ta 60) from the third horizon. Scale bar in C represents 10 mm. Colour online.
conditions of significantly reduced visibility caused by bottom water turbidity. The number of lobsters moving in single queues along the scent path (= urinal trail) is variable, reaching a few to several dozen individuals usually during day to day movements, and hundreds or even thousands of individuals in seasonal migrations (Booth 1997).

Trilobite migratory queues controlled by chemotaxis

In the case of Trimeroccephalus chopini queues, it is probable that trilobites moved one after another following chemosensory cues because T. chopini was eyeless and is regarded as having had no alternate photoreceptors. Therefore, T. chopini queues are recognized as the first fossil record of possible chemotaxis, and these lines are interpreted as the oldest known migratory queues. We suggest that the trilobites were undergoing mass migrations to spawning-grounds during reproductive periods.

This hypothesis is supported by the relatively small but variably sized specimens forming queues, demonstrating putative dimorphism with approximately equal numbers of the two dimorphs, and by comparison with modern analogues. There is abundant evidence for possible aggregative moulting and mating behaviour in phacopid trilobites (Speyer & Brett 1985; Brett et al. 2011; Brett et al. 2012). Mass occurrences of Ordovician trilobites have also been explained as a result of mating behaviour (Karim & Westrop, 2002; Gutiérrez-Marco et al. 2009). The repeated occurrences of species-segregated clusters of carcasses and moult ensembles, of similarly sized individuals in particular facies in the Middle Devonian Hamilton Group suggests that the trilobites migrated to particular breeding grounds prior to mass moulting and spawning as in certain extant peracarid crustaceans (Speyer & Brett 1985).

Such mating grounds might also become trilobite ‘nurseries’ (Paterson et al. 2007). Modern analogues of this phenomena are represented by ‘nursery grounds’ of the horseshoe crabs (e.g. Tachypleus tridentatus Leach and Limulus polyphemus Linnaeus (Carmichael et al. 2003)). ‘Limulid nurseries’ are also described from the Upper Jurassic of Poland (Kin & Blażejowski 2014; Blażejowski 2015), and similar ‘nurseries’ observed in some echinoderms are widely discussed by Radwański et al. (2012, 2014).

The latter suggestion appears to be supported in the case of the Kowala trilobites by the occurrence of a number of small, sphaeroidally or discoidally enrolled T. chopini specimens (Fig. 4A–F) in situ within each of the three horizons with the queues. All of these enrolled individuals represent mersapid stages with 3–7 thoracic segments, i.e. juvenile forms of T. chopini. Thus, the juveniles may represent remains of a ‘trilobite nursery’ and the T. chopini queues formed by sexually mature individuals (i.e. holaspids in strict morphological terms) may represent migration to the spawning area during reproduction cycles. It should be emphasized that the largest

FIG. 3. Migratory queue of Trimeroccephalus chopini Kin & Blażejowski, 2013 from Kowala Quarry (Holy Cross Mountains). Schematic drawing of three marly shale surfaces exposing the longest T. chopini queue (formed by 19 specimens; Kow/Ta 3) as extracted from the first of studied horizon (left) and close-ups of the best preserved fragments (right). Scale bar represents 50 mm. Colour online.
<table>
<thead>
<tr>
<th>Queue characteristics</th>
<th>Kow/Ta 3 (Fig. 3)</th>
<th>Kow/ Ta 19</th>
<th>Kow/ Ta 22</th>
<th>Kow/ Ta 23</th>
<th>Kow/ Ta 45</th>
<th>Kow/ Ta 47</th>
<th>Kow/ Ta 59</th>
<th>Kow/ Ta 60 (Fig. 2C)</th>
<th>Kow/ Ta 63</th>
<th>Kow/ Ta 77</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of individuals</td>
<td>19</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>10</td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>Individuals with 9 thoracic segments</td>
<td>8</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Length of individuals with 9 thoracic segments (mm)</td>
<td>5/11/12/9/10/~10/9/11</td>
<td>9/11</td>
<td>10/7/11</td>
<td>10/8/~11/10</td>
<td>11</td>
<td>11</td>
<td>2</td>
<td>2</td>
<td>5/10/10/12/9/10</td>
<td>9/10/8/~10/11</td>
</tr>
<tr>
<td>Individuals with 10 thoracic segments</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Length of individuals with 10 thoracic segments (mm)</td>
<td>15/17/14/~19</td>
<td>17/17/18</td>
<td>15/17</td>
<td>13</td>
<td>7/13/17</td>
<td>11/11/9/10/10/16</td>
<td>15/18/15</td>
<td>14/14/15/~14/12/17</td>
<td>14/14/15/17</td>
<td>13/14/17/14/14</td>
</tr>
<tr>
<td>Additional data for incomplete individuals (width: length of cephalon; mm)</td>
<td>5:3/~7:5/6:4/~5:3 &amp; three small to semi-large partially preserved thoraces</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>5:3</td>
<td>–</td>
<td>86 &amp; 7:5</td>
<td>~7:5 &amp; single part of thorax</td>
<td>–</td>
<td>5:3 &amp; ~5:3</td>
</tr>
</tbody>
</table>
number of segments observed in the thorax of *T. chopini* was 11 (Kin & Błażejowski 2013). Variable numbers of segments in holaspid trilobites is very rare, but have been demonstrated in the unusual form *Aulacopleura konincki* (Hughes & Chapman 1995). In the latter, dimorphism is ruled out as the segment numbers vary from 18 to 22.

If the unique queues formed by *T. chopini* discussed herein were strictly connected to periodic migrations for breeding, it could be assumed that *T. chopini* reached maturity during the 9- or 10-segmented stage. It also means that the sexual maturity of *T. chopini* was not necessarily combined with morphological stabilization of their exoskeletons, as revealed essentially by the occurrence of a stable number of trunk segments. It is associated with the transition between two main ontogenetic phases: from the morphologically variable larval (meraspid) period to the morphologically stable post-larval (holaspid) period, i.e. from anamorphic to epimorphic phases (Hughes et al. 2006; Crónier 2011). Thus, the results of this study provide a possible example of sexually mature trilobites, forming unique migratory queues and represented by non-holaspid individuals (i.e. non ‘adult-type’ forms, in terms of widely accepted morphological classification).

The variation in thoracic segment number could simply represent an unusual case of meristic variation of segment number within a species, or different moult stages. Alternatively, and more probably, the 9- or 10-segmented individuals both represent holaspids, but male and female dimorphs respectively. The fact that both 9- and 10-segmented forms show a substantial and similar range of variation (5 mm for 9-segmented forms and 7 mm in 10-segmented forms) suggests that each morph is not simply a different growth stage. Rather, each form occurs as both smaller and larger sized individuals, a range much larger than that found in a single meraspid instar of any known trilobite. Furthermore, the earlier meraspid forms, up to stage 8, are represented by the minute enrolled specimens, so there was a very large size difference between meraspid stage 8 and stage 9 or 10, suggesting that once one or the other of these segment numbers was achieved it remained stable through a substantial size range, most likely representing several moult episodes.

Other forms of probable sexual dimorphism in trilobites have been documented, including the presence of prelabellar bulbs, being possible brood pouches (Fortey & Hughes 1998), and median cephalic bulbs and spines in raphiophorids (Knell & Fortey 2005). These morphological features can be logically related to functional differences between sexes (e.g. brood pouches in females) or sexual selection. Conversely, it is difficult to conceive of

**FIG. 4.** Two examples of juvenile enrolled trilobites representing a meraspid stage, occurring in the upper parts of two horizons with *Trimeroccephalus chopini* queues. A–C, example of a small, enrolled specimen found in horizon 1. D–F, slightly larger enrolled specimen from horizon 2; note the white arrow marking siderite filling the enrolled specimen. G, backscattered electron image of the sediment just beneath the skeleton of one of the trilobites in the *T. chopini* queue with a place of composition analysis marked with arrow; note the amount of iron oxide (white) crystals pseudomorphs after pyrite and the stable carbon and oxygen isotope compositions for the sediment matrix. H, *T. chopini* exuvium; note that the δ¹³C values and δ¹⁸O isotope values for the sediment from underneath the exuviae are identical to those for the sediment adjacent to the trilobite queue. Scale bars represent 1 mm (A–C, G); 2 mm (D–F); 4 mm (H). Colour online.
functional distinctions in forms with one more or less segment. Possibly, this was simply related to size differences between sexes, but, as yet, we have no more plausible explanation. For this reason, we must be slightly tentative in ascribing this dimorphism to sexual differences. Nonetheless, considering the cohort of trilobites occurring in queues as a whole, the ratio of 9- to 10-segmented individuals is very nearly 1:1. While sex ratios in some organism populations are significantly different from unity, the preservation of 1:1 ratios of morphotypes is strongly suggestive of sexual dimorphism. Interestingly, the vast majority of contemporary arthropods become sexually mature exactly after entering into the epimorphic phase (Minelli 1992, 2003; Minelli et al. 2006). This occurrence of dimorphism in segment number is, to our knowledge, unique among trilobites and its functional significance, if any, is not known, although differences in mean size between sexes are common.

Sedimentary characteristics of the bottom sediment for the migratory queues of T. chopini indicate (see Radwański et al. 2009) a low energy hydrodynamic regime. Typical parallel to low-angle cross lamination and occasional hummocky cross stratification of the carbonate silt indicate a low energy setting affected by occasional storms. An abundance of remains of primitive plants (i.e. psilophytes) provides evidence for close proximity to land; however, these remains may have been transported offshore to settle out in relatively deep water, where dysoxic conditions favoured their preservation.

Mass mortality of Trimerocephalus chopini

The most striking feature of the examined trilobite queues is the preservation of the members of the queue in their life positions suggesting instantaneous mortality. A few trilobite individuals in the queues exhibit slightly flexed postures, suggesting incipient but incomplete enrollment, a plausible defensive behaviour for trilobites. The occurrence of fine-grained pyrite and slightly negative δ13C values for the sediment adjacent to trilobite queues, as well as that directly beneath the carcasses, strongly suggests bacterial decay of rapidly buried trilobite soft parts in the sulphate reduction zone. Anaerobic degradation of organic matter underneath the trilobite skeletons may have increased alkalinity sufficiently that pore fluids became supersaturated with respect to calcium carbonate causing precipitation of cements.

Small, enrolled T. chopini exoskeletons are filled either by siderite (δ13C = −1%oo and δ18O = −2.5%oo), or sediment of almost identical appearance to the sediment beneath the skeletons of queuing trilobites, forming concretionary infillings within the enrolled skeletons. Both the sediment inside the enrolled trilobites and that forming concretions contain abundant iron oxide pseudomorphs after pyrite crystals; both also display δ13C values of ~−0.5%oo. The enrolled specimens of T. chopini suggest that they had time to take defensive action, i.e. enrolling the body to protect sensitive ventral respiratory surfaces, so their death was not as sudden as that of trilobites in the queues.

Any hypothesis for the preservation of these queues must explain the nearly synchronous mortality of many individuals slightly prior to abrupt burial. We suggest that the initial affect of storms may have been to stir up anoxic, sulphide-rich sediment slightly upramp from the site of mortality, producing thin suspensions of toxic, turbid water. The most likely scenario for sudden death of both the adult and juvenile T. chopini involves suffocation, hypercapnia (excess CO₂) and/or toxicity of sulphidic waters. Seemingly, these trilobites died literally in their tracks but the carcasses were then subject to minor, incipient post-mortem decay, without transport, prior to rapid burial. We suggest that clouds of suspended sediments subsequently blanketed the seafloor, perhaps as a result of fallout of flocculated muds in the aftermath of the same storm that had killed the animals.

Juvenile forms of T. chopini could attain fully enrolled postures, perhaps because small forms were more tolerant of anoxic/sulphidic conditions compared to adult individuals, as has been demonstrated in experiments (see Holman & Hand 2009) carried out on ghost shrimp of the species Lepidophthalmus louisianensis Schmidt. Thus, these juveniles survived long enough to respond to the toxic stimulus by enrollment.

CONCLUSIONS

Results of our research demonstrate that repetitive migratory behaviour had already evolved among marine animals by at least the mid-Palaeozoic Era. We infer that the breeding strategy for the blind trilobite Trimerocephalus chopini Kin & Blażejowski 2013 included mass migration to spawning-grounds; the mass migrations in queues were likely coordinated by primary chemosensory phenomenon, as in some modern crustaceans. An important argument related to periodic migration of T. chopini to the breeding areas is the co-occurrence of numerous enrolled juveniles, which occur in each queue horizon; these abundant juveniles could record ‘trilobite nurseries’. Moreover, individuals of T. chopini forming migratory queues do not show a fixed number of thoracic segments. A plausible explanation for the 9- and 10-segmented variants, considering their nearly 1:1 ratio, is that they represent sexual dimorphs in a single species; these two morphotypes each show considerable and overlapping size ranges, although the 10-segmented morph is generally larger.
As to causes of sudden death of the described blind trilobites, we suggest poisoning by hydrogen sulphide, which is very diffusive and highly toxic, and/or hypercapnia, owing to carbon dioxide released from sediment, replacing oxygen in the bottom waters. Regardless, the similar state of in situ preservation of these blind trilobites suggests almost simultaneous death of all of the individuals (both enrolled juveniles and sexually mature adults arranged in the queues). Abrupt burial of *T. chopini* populations followed very shortly after the mass mortalities, probably from fallout of flocculated muds stirred up by storms (Type 1 assemblages of Brett et al. 2012). This must have been a recurrent phenomenon in this area during the Late Devonian because at least three occasions of storm burial overlapped with reproductive periods of *T. chopini* to produce similar queues at three distinct horizons.

Finally, we conclude that chemotaxis may have functioned as a long-term macroevolutionary process controlling reproductive behaviour of arthropods, the largest known phylum of animals on Earth.

Acknowledgements. Most of the work presented in this paper, including field and laboratory studies and the idea and overall design of research, were initiated by Adrian Kin who passed away before the completion of the final draft of this paper. Błażej Blażejowski, Carlton E. Brett and Andrzej Radwański accepted responsibility for the validity of data and conclusions presented herein. Warmest thanks are expressed to Urszula Radwańska (University of Warsaw) for many helpful suggestions during the early phase of this investigation. Comments and criticism supplied by Tammie Gerke greatly improved the quality and content of this manuscript. We would like to thank Adam T. Halamski (Institute of Palaeobiology, PAS) for assistance with statistical analysis. And last but not least, we wish to acknowledge Lisa Amati (NY State Museum, Albany), Sally Thomas (The Palaeontological Association) and one anonymous reviewer for his critical review and very helpful comments that improved the manuscript.

Editor. George Sevastopulo

REFERENCES


BŁAŻEJOWSKI ET AL. : ANCIENT ANIMAL MIGRATION 751
