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Queues of blind phacopid trilobites *Trimerocephalus*: A case of frozen behaviour of Early Famennian age from the Holy Cross Mountains, Central Poland

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ABSTRACT:

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An assemblage of blind phacopid trilobites of the genus *Trimerocephalus* McCoy, 1849, representing either the species *Trimerocephalus mastophthalmus* (Reinhard Richter, 1856) or its allies (possibly, a new species), from an Early Famennian (Early Marginifera Zone) marly sequence of the Holy Cross Mountains, Central Poland, is composed of well organized single-file queues. The trilobites in the queues appear almost intact, having been preserved in the position they kept when forming the queues, and are interpreted showing migratory behaviour known in various present-day arthropods, but unreported from the fossil state. This queuing was induced by environmental stress caused by a dramatic drop in sea level, temporarily leading to emersion. The preservation of the queues at omission horizons is thus ascribed to a mass mortality event, caused by subaerial exposure. The trilobites were suffocated and fossilized in a mortal spasm, and finally blanketed by calcareous ooze when inundated at a highstand. The assemblage of trilobite queues represents a unique example of frozen behaviour and a snapshot of the geological past.

Key words: Trilobites; Frozen behaviour; Migratory queues; Eco-taphonomy; Mass mortality; Famennian; Holy Cross Mountains; Poland.

INTRODUCTION

The aim of the present paper is to describe unique aggregates of Upper Devonian (Lower Famennian) blind phacopid trilobites of the genus *Trimerocephalus* McCoy, 1849, organized in single-files of reasonable length comprising up to 13 specimens lined up unidirectionally. These are preserved in two horizons of a thick sequence of almost unfossiliferous marlstones from the Holy Cross Mountains, Central Poland (see Text-figs 1-2). Both the mode of aggregation of the specimens and their state of preservation are quite dissimilar to any of the hitherto reported cases of trilobite mass-occurrences all over the world.

To characterize the aggregates, the term queue is used herein, instead of pod which was earlier used by Warner (1977, p. 117) for irregular or spherical heaps formed by king crabs. On the other hand, the term queue has already been used by Herrnkind (1969, 1975, 1983, 1985) to describe the migratory behaviour of the present-day American Spiny Lobster, *Panulirus argus* (Linnaeus).

Former reports on mass-aggregated trilobites, especially the important studies by Speyer and Brett (1985) and Speyer (1987, 1990), concerned patch-like accumulations, either of 'fully' preserved specimens (?live, or dead), or of moults. The single-file queues described herein represent live trilobites entombed while migrating, and frozen by rapid burial. Environmental conditions under which the trilobites lived/migrated and died will be considered, because comparisons with the migratory behaviour of extant arthropods (decapod crustaceans, xiphosurans, freshwater amphipods, insects) do not offer satisfactory analogues.

The trilobite queues, discovered by one of us (AK) in the late 1990s, became a subject of considerable educational interest (Radwańska 1999a, pl. 19, fig. 3; see also Kin and Radwański 2008, p. 44).

LOCATION DATA

The Famennian sequence that yields the trilobite queues is exposed within the Kowala Quarry in the village of Kowala, situated in the western part of the Holy Cross Mountains, Central Poland, some 10 km south of the town of Kielce (see Text-fig. 1). The Kowala Quarry is immediately adjacent to the classic Kowala railway section, both of which were thoroughly studied by Szulczewski (1971; updated in 1995, 1996, 1998).

The queues occur near the base of the local lithostratigraphical Unit I of Berkowski (1991), to which Szulczewski (1995, 1996, 1998) assigned an Upper Marginifera Zone age. An analysis of the conodont fauna performed for this study by Professor Zdzisław Bełka (University of Poznań) clearly shows that the queue-bearing part of Unit I actually belongs to the Lower Marginifera Zone.

Unit I is composed of pale grey marlstones, at some horizons replete with calcareous nodules, all weathering with a yellowish tint. The unit is about 20 m thick, and its macrofossil content was claimed to be limited to the presumably pelagic bivalve *Guerichia* (see Szulczewski 1995; Berkowski 2002, p. 8). All the abundant faunas that are well known from this quarry (see review by Berkowski 2002) came from lithostratigraphic intervals other than Unit I.

The marlstones composing Unit I are exposed in part of the northern margin of the quarry (see Text-figs 1–2), along the wall parallel to the strike of beds dipping towards that wall, and in its lower part are covered by talus (see Text-fig. 2). Such an exposure provides very limited access to the trilobite-bearing strata in which the queues were recognized in two distinct horizons, about 1.2 metres apart. Of these, the more prolific appeared to be the lower one (1 in Text-fig. 2B) which yielded the majority of the well-organized queues (see Text-fig. 3 and Pls 1–5), collected within an about 2 to 3 cm interval of the marlstone sequence. The upper horizon (arrowed as 2 in Text-fig. 2B) yielded only some disarranged queues (see Text-fig. 8).

Berkowski (1991) documented two horizons of mass-aggregated *Trimerocephalus* exuvia, interpreted as having been left by infaunal (burrowing) specimens. These two horizons are located within the boundary beds of Unit J and K (solely in K according to Berkowski 2002, p. 8), about 35–40 metres above the beds with the trilobite queues. Neither the behavioural nor the taphonomic interpretation given by Berkowski (1991) is compatible with those apparent from the present study of the queues occurring in the lowest part of Unit I.

THE QUEUE MATERIAL

All the trilobite queues are distributed on the top surface of the marlstone layers. As the queue-bearing marlstones are more or less compact and brittle, having been densely cracked by a complex joint pattern, the collected material consists of relatively small slabs that vary in size from small pieces up to those as large as a tile. Of the slabs collected, almost all contain queues that reach the two opposite edges of the slab. The largest illustrated specimens (Pl. 3, Fig. 1; Pl. 4, Figs 1–2; Pl. 5, Figs 1–2) thus represent only parts of supposedly much longer queues.

In view of the limited exposure, it is impossible to attempt to decipher the orientation of the queues in space, that is over a temporary seafloor.

Some of the trilobites are also present on the top surface of calcareous nodules, where they occur either singly, or in 'imperfectly' organized queues (see Text-fig. 3).

Taking into account the fact that most of the queues studied were obtained from a thin marlstone interval (Horizon *1* in Text-fig. 2B), they are thought to represent either one, or several successive populations of trilobites showing the same behaviour and burial conditions. Consequently, the collected material of these queues is treated as one entity in the following description. Some specimens of disorganized queues (see Text-fig. 8) from Horizon *2* are treated separately.

The material under study is housed in the Collection of the Geoscience Friends Association '*Phacops*' in Łódź, and registered under Catalogue Numbers Kow TA 1-78; these registration numbers refer to the sampled slabs regardless of the number of trilobite individuals aggregated in queues.

PRESERVATION OF THE TRILOBITE SKELETONS

The trilobite exoskeletons in the majority of specimens are not fully exposed on the sediment surface. This is due to the overlapping of specimens in pairs (e.g., Pl. 1, Figs 3–7) and shorter or longer queues (e.g., Pl. 3, Fig. 2 and Pl. 5, Fig. 1), or forming jams to a variable extent (e.g., Pl. 2, Fig. 5 and Pl. 4, Fig. 2), and even a stacked heap in an extreme case (Pl. 3, Fig. 3).

Apart from the occipital fracture, along which the cephalon may be partly displaced (e.g., Pl. 1, Fig. 3; Pl. 2, Figs 1a and 4b), almost all the specimens bear either the pygidium alone, or together with last posterior thoracic segment(s) turned under the body. As a result, there are only a few straight specimens available for counting the number of segments. The maximum number of 11 segments is observed rarely (*e.g.*, Pl. 1, Figs 2b and 4c; Pl. 4, Fig. 1a), and commonly 9 or 10 segments are exposed. The smallest specimens with the same number of segments (Pl. 1, Figs 1–3) are treated as phenotypic variables, possibly stunted (dwarfish) for unknown reasons.

The mode of preservation of the trilobites in the queues (see Text-fig. 3 and Pls 1–5) indicates their burial *in situ*, perhaps while still alive (*in vivo*) or immediately after death. The posture of the specimens is interpreted as identical with that they maintained while still alive on the sea bottom. Some deviations from an ideal life position are thought to have resulted either from the death agents, or from the burial conditions, as follows:

(*i*). Turning down of the pygidium, alone or with a few adjacent thoracic segments, being effected by the mortal cramp of the body (most clearly seen in: Pl. 2, Figs 2b, 4b, 4c; Pl. 3, Figs 1e, 2c, 2e; Pl. 4, Figs lc, le).

(*ii*). Indistinct transverse (lateral) turning down of pleurae (e.g., Pl. 2, Figs 4b, 4c; Pl. 4, Fig. 1c; Pl. 5, Fig. 1d) being effected by the same cramp;

(iii). Swelling of the rhachis, which often appears to be intumescent sagittally (e.g., Pl. 2, Figs 2b and 4b–4c; Pl. 3, Fig. 1e; Pl. 4, Fig. 1e), being presumably effected by post-mortal degassing of corpses (osmotic uptake, see Hof and Briggs 1997);

(iiii). Occipital fracturing and displacement of the cephalon resulting from a diagenetic event of compaction (‘compactional distortion’) when the still alive specimens or the corpses became covered by a sediment load from which those still alive could not escape.

As a result of the cramp proceeding both sagittally and transversally, some specimens acquired an almost circular outline (e.g., Text-fig. 3c; Pl. 1, Figs 6b, 6c; Pl. 2, Figs 1b, 2a, 6d, 6e; Pl. 5, Fig. 1e; also sketch in Text-fig. 1B).

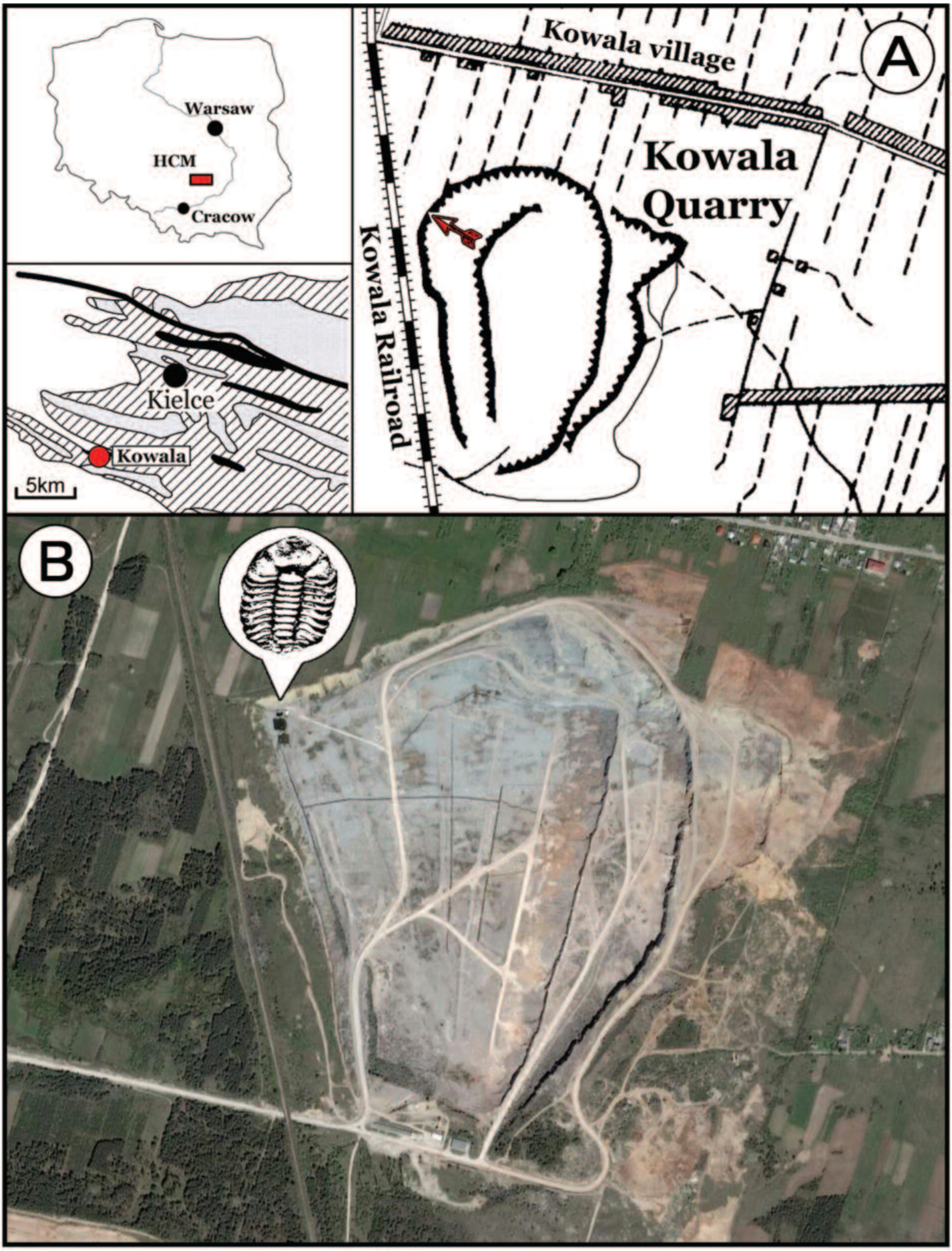
In some specimens, where a part of the exoskeleton has become chipped away from the pleurae, the appendages (exo- and/or endopodites) may be detected (e.g. Pl. 2, Fig. 2b at left); these are still in need of careful preparation to avoid damage of the queues during further study.

TRILOBITE TAXONOMY

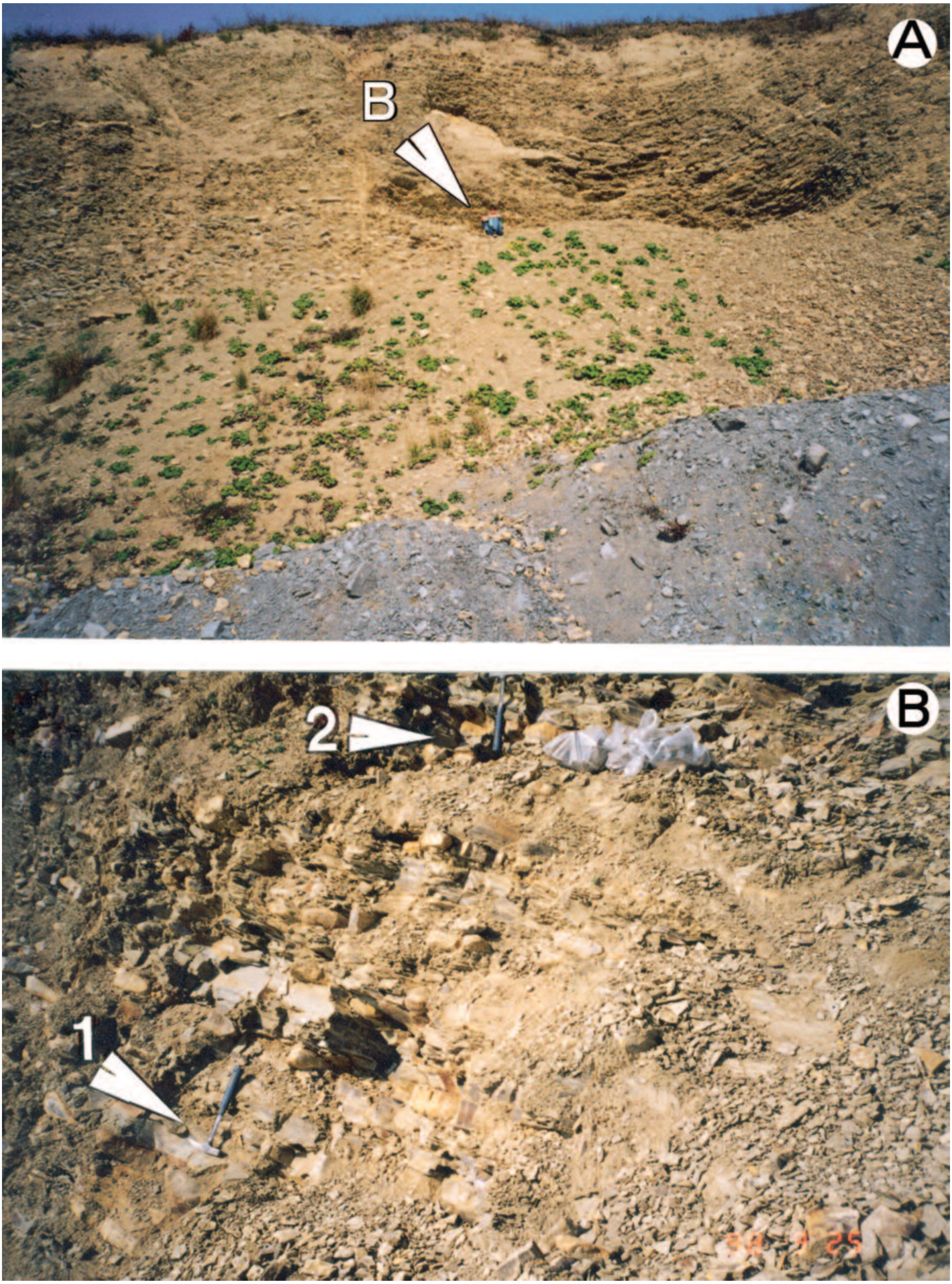
The trilobites forming the queues are regarded as monospecific, in analogy to the present-day crabs that tolerate only conspecific individuals when they aggregate (see Warner 1977, p. 117). A problem arises, however, in determining the species in question.

The trilobite exuvia recognized in the Kowala sequence by Berkowski (1991) were classified by him as a separate species, *Trimerocephalus interruptus* Berkowski, 1991, which may actually represent (see Berkowski 1991, p. 261) different populations of *Trimerocephalus polonicus* Osmólska, 1958, known from scanty material (6 cephala) from a coeval succession in the Kadzielnia Quarry at Kielce. The dense microgranulation of the cephalon, conspicuously displayed by many well preserved specimens studied (see e.g. Pl. 1, Figs 4b, 4c, 5d, 6a; Pl. 2, Figs 1a, 4b; Pl. 3, Fig. 1b), is very different from that of the dispersed tubercles in *T. polonicus* shown by Osmólska (1958), and it is similar to that of *T. mastophthalmus* (Reinhard Richter, 1856). As long as the taxonomic relationships of these three species and others from neighbouring countries remain unclear (see discussion by Osmólska 1958, p. 135; and Berkowski 1991, pp. 260–261), the trilobites composing the queues are tentatively accommodated in the last of the three species listed, that is *mastophthalmus* established by Reinhard Richter (1856) and thoroughly revised by Rudolf and Emma Richter (1926). This species, the type species for the genus *Trimerocephalus* McCoy, 1849, is widely known from the Lower Famennian of Europe and Asia (see Crônier 2003).

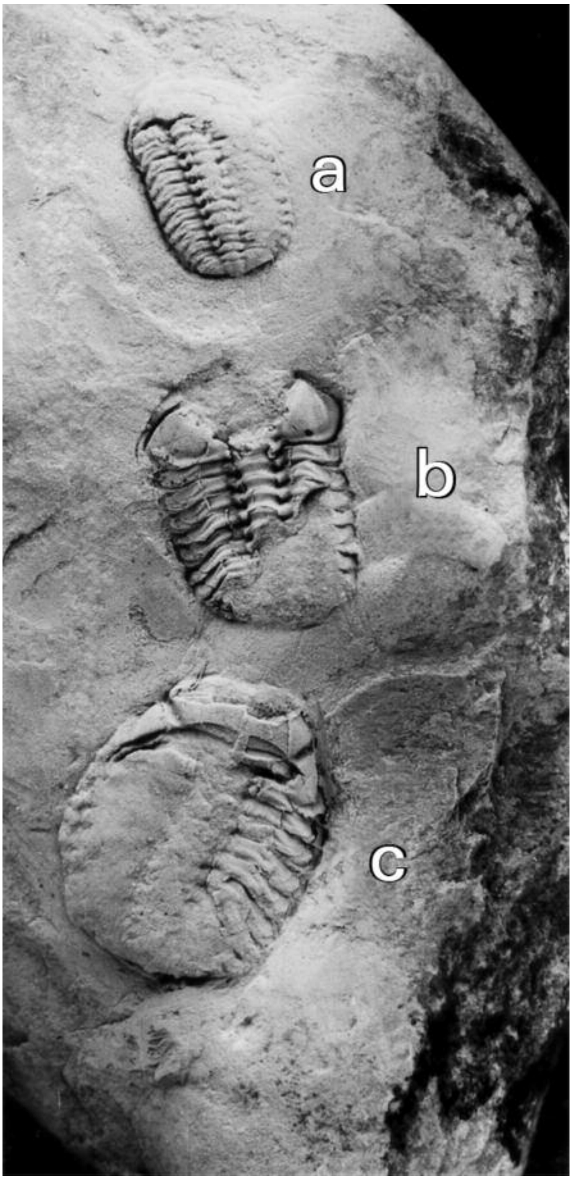
The individuals composing the queues seem to share their features with at least three species of *Trimerocephalus*. A description of their anatomy lies, however, beyond the scope of this report. The assemblage, still under further study, and totalling some two hundred almost completely preserved/exposed exoskeletons, is seemingly the richest ever collected. Study of this assemblage may eventually enable recognition of the morphological diversity of one definite *Trimerocephalus* species (cf. Crônier and Feist 1997), including its possible sexual dimorphism (cf. Hu 1971, pp. 122–124) and phenotypic plasticity.



Text-fig. 1. Location of the trilobite queues studied (inserts indicate its position in Poland and in the western Holy Cross Mountains): **A** – Sketch-map of Kowala Quarry (adapted from Berkowski 1991 and 2002), **B** – Satellite photo of the Quarry; the queue-bearing sequence is indicated by an arrow (see Text-fig. 2)



Text-fig. 2. The trilobite queue-bearing sequence (Unit I of Berkowski 1991, 2002) exposed in Kowala Quarry: **A** – General view of the westernmost part of the northern quarry-wall ; **B** – Close-up, to show the two horizons (*1* and *2,* arrowed) yielding the queues (loaf-shaped or lenticular calcareous nodules are pronounced; some of them are mud-cracked, see Text-fig. 7A)



Text-fig. 3. Incompletely organized queue composed of three trilobites marching in head-to-tail position around the edge of a calcareous nodule (see explanation in the text); taken × 3

PREVIOUS RECORDS OF TRILOBITE AGGREGATION AND ORIENTATION

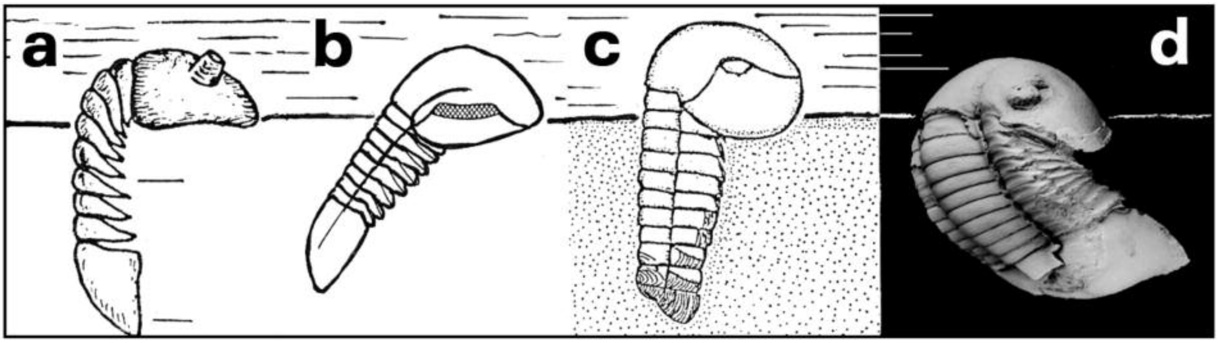
The subject of aggregation in trilobites concerns both their life activity as well as the accumulation of corpses or successive exuvia. In both, an orientation of specimens may also appear due either to their mode of life, or to dynamic agents acting *post mortem* (current lineation, for example). However, it is not always possible to determine the cause of aggregation unequivocally.

Aggregation in trilobites was previously documented by Speyer and Brett (1985) and Speyer (1987, 1990), based primarily on Middle Devonian (Givetian) material from the Hamilton Group of New York State, U.S.A. These studies delivered the first convincing arguments that monospecific clusters were behavioural in nature, being formed for moulting prior to *en masse* copulation. Such *body clusters* (of corpses), were composed of age-segregated specimens with fully preserved exoskeletons, in contrast to the *moult clusters* composed of disarticulated exuvia.

Both Speyer and Brett (1985) and Speyer (1987, 1990) have also reviewed and/or briefly commented on earlier reports on aggregated trilobite produced by hydrodynamic agents (current transportation, or lagging due to winnowing). All these aggregations formed heaps or patches, with no preferred orientation of specimens. The same applies to the three examples of trilobite mass-aggregations presented by Levi-Setti (1993) and suggested to represent either mating assemblages (Levi-Setti 1993, pls 134 and 199) or accumulated exuvia or reworked remains (Levi-Setti 1993, pl. 200); these aggregations, with no orientation of the cephala, do not differ from hydrodynamic accumulates.

A peculiar case of orientation and possible aggregation is found in some of the large-eyed trilobites. Such trilobites, which were not uncommon in the early Palaeozoic (Cambrian–Ordovician), have been preserved semi-buried, more or less vertically in the seafloor, with their cephalon stretched out on the sediment surface. The most spectacular examples (see Text-fig. 4) were interpreted as cases of the preservation of trilobites in life position (Finch 1904, Ager 1963, Bergström 1973, Stitt 1976; see also Westrop 1983). These examples may be regarded as a case of frozen behaviour of the predatory trilobites when they were scanning their foreground ('onwards'), as already concluded by Finch (1904, p. 181). In a unique rock-specimen described by Finch (1904, pl. 14; see also Ager 1963, pp. 90–91), fifteen specimens in a group were oriented unidirectionally with their cephala facing the suggested current carrying the expected prey. In such aggregations, referred to a swarm- or herd-mode of life, the orientation involved the sense of vision; the swarming individuals were not in contact but dispersed on the sea floor.

Fortey and Owens (1999), when analyzing the feeding behaviour in trilobites, interpreted some linear aggregations of highly disordered exoskeletons (see Fortey and Owens 1999, p. 442 and fig. 10) as formed during the search for food. Similarly disordered were Ordovician agnostids, arrayed in a linear trail (Pek 1977), whose interpretation as a possible attachment of



Text-fig. 4. Examples of frozen behaviour in trilobites, presumably expecting the prey to pass by: **a** – *Ptyocephalus vigilans* (Meek); Upper Ordovician, Iowa, USA; based on Finch (1904, p.14, figs 1–4), adapted from Ager (1963, fig. 5.10), for taxonomy see Stitt (1976, p. 571); **b** – *Panderia megalophthalma* Linnarsson, 1871; Ordovician; after Bergström (1973, fig. 13); **c** – *Stenopilus pronus* Raymond, 1924; Upper Cambrian, Oklahoma, USA; adapted from Stitt (1976, fig. 6); **d** – *Illaenus sarsi* Jaanusson, 1954; Lower Ordovician, Slemmestad near Oslo, Norway; original photo, natural size (cf. life habit in Bergström 1973, fig. 14)

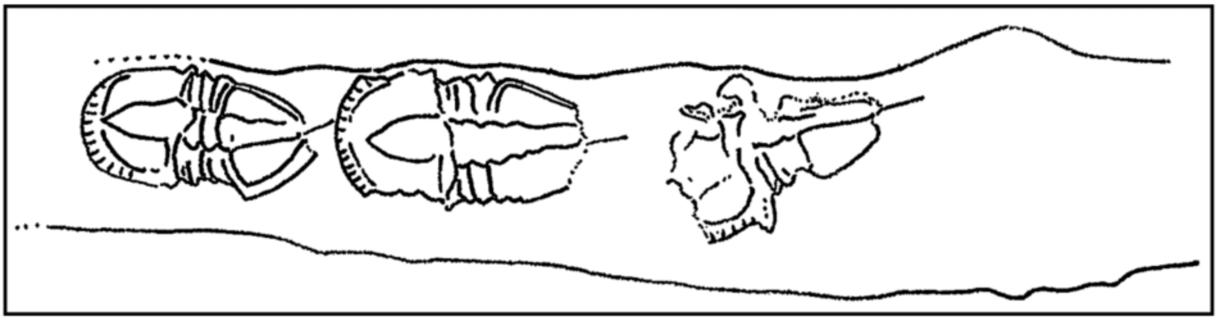
specimens to an algal thallus was accepted by Fortey and Owens (1999), but objected by Chatterton *et al.* (2003, p. 170).

Suzuki and Bergström (1999) discussed in detail the mode of life of trilobites from Upper Ordovician buildups of Sweden, the crevices in which acted either as refuges for cryptic behaviour (e.g. for moulting) or as preservational traps, in both cases leading locally to aggregation of exoskeletons.

Another type of trilobite aggregation, of up to a few specimens, was reported by Davis *et al.* (2001) from Ordovician and Silurian orthoconic nautiloid shells, and interpreted as formed by live trilobites which used these refuges for shelter from potential predators. No evidence has, however, been given that these trilobites were alive when buried. In the internal moulds of the nautiloid body chambers, the trilobites are preserved with their dorsum outwards (see Davis *et al.* 2001, figs 1–4 and 8), which evidences their being corpses settled upside-down on the bottom of body chambers when these were still empty and had become a taphonomic trap. Otherwise, if live specimens had entered a chamber, they would have been preserved with their venter in contact with the inner wall of the chamber, and thus could not have been exposed by their dorsum on the exterior of the internal moulds of the chambers (see discussion by Brett 1977, p. 1043 and fig. 2A).

The problem of cryptic behaviour (including burrowing) in Cambrian-to-Silurian trilobites has been widely studied by Chatterton *et al.* (2003), who regarded it as resulting from their ability to hide while moulting or scavenging. In a spectacular specimen, they show a case of three small trilobites entombed in a priapulid worm tube from the Burgess Shale (see Chatterton *et al.* 2003, pl. 1, fig. 2; sketched herein as Text-fig. 5): these trilobites are arranged head to tail, which was noted by Chatterton *et al.* (2003, p. 170) as the then only known example of such orientation in the fossil state. [The live trilobites entering a narrow worm tube, and not being able to withdraw, would have been entrapped in the same way as present-day eels in a long fish-pot netted by poachers].

Of the diverse types of trilobite aggregation, reported by Chatterton and Fortey (2008) from the Or-



Text-fig. 5. An earlier reported example of trilobites arranged head-to-tail: Three specimens of *Pagetia bootes* Walcott, 1916, in a tube of the priapulid worm *Selkirkia columbia* Conway Morris, 1977, from the Burgess Shale (Middle Cambrian of British Columbia, Canada), × 5; sketched *from* Chatterton *et al*. (2003, pl. 1, fig. 2) dovician of Morocco, the only two that are structurally similar comprise two specimens of *Ampyx* 'rows', the interpretation of which remains, however, highly equivocal (see Chatterton and Fortey 2008, p. 76 and pl. 1, figs 6–8). The idea of tunneling by the trilobites having either entered, or been swept into, foreign burrows (that acted as a shelter or a preservation trap), which has recently appeared in the relevant literature (Cherms *et al.* 2006, Chatterton and Fortey 2008, Paterson *et al.* 2008, Gutiérrez-Marco *et al.* 2009), cannot be applied to the queues in this study. In these queues, all the specimens are oriented head to tail, and there is no evidence either of their cryptic/burrowing activity or of physical accumulation; all bear complete exoskeletons and are preserved in the position they maintained when alive on the sea bottom.

Furthermore, of previous reports of aggregation in trilobites only that given by Finch (1904) is recognized as relating to live specimens. Moreover, preservation in life position but not evidently during life, recognized in three other cases (Bergström 1973, Stitt 1976; authors'own material, Text-fig. 4d), is still a very rare phenomenon in any trilobites.

AGGREGATION IN PRESENT-DAY ARTHROPODS

Aggregation in present-day arthropods, both aquatic and terrestrial, is not *per ipse* peculiar, and is well known in some decapod crustaceans, xiphosurans, freshwater amphipods, and insects.

In crabs, a tendency towards a gregarious mode of life in some species results in population densities that may reach the extreme figures of 1,500 to 3,000 mature individuals per square metre (see Thorson 1957, p. 519; Bishop 1986, p. 329).

The above example is one of a high population density where the individuals are widely dispersed. Much more significant are cases of local aggregations, where many specimens accumulate in a restricted spot. As concisely reviewed by Warner (1977, pp. 116–117), the present-day European Spider Crab *Maia squinado* Herbst occasionally forms conical heaps, up to several feet in height, containing a large number of adult individuals (1,000 or more), that may remain stationary for a few months. The heaping has a protective function, particularly while moulting and mating, during which smaller individuals and females are kept inside a heap guarded by the males sitting on top or around its edges. This protective function is also realized by giving the impression of being much larger, and thus discouraging predators when attacked, as well as by the availability of many more eyes to watch out for possible predators (see also Parrish and Edelstein-Keshet 1999).

In present-day crabs examples of both social-life behaviour and territorialism are known. As reviewed by Warner (1977, pp. 116–118), social-life behaviour is typical of the genus *Uca* living in colonies, while territorialism is found in the terrestrial *Cardisoma*. The latter may also live in small colonies, whose members are able to recognize their neighbours as belonging to the colony and will defend their territories against strangers. The social mode of life in crabs is also apparently effective when foraging in groups for better exploration of the food resources/areas.

Semi-terrestrial crabs seasonally form myriad armies of individuals which march in fairly disorganized crowds towards the beaches and shallow shores (see Warner 1977, p. 118). This appears to be a case of migratory behaviour related to seasonal reproduction.

The most important example of organized aggregation is that observed in the American Spiny Lobster *Panulirus argus* (Linnaeus), which occasionally migrate in long files. This is certainly an unforgettable sight, when thousands of spiny lobsters (estimates range up to 200,000 specimens; see Herrnkind 1983, p. 92) march unidirectionally in single-file queues, both day and night for several days. One such queue in a 10-m depth of water west of Bimini, Bahamas, was photographed by Herrnkind (1985, fig. 1). As studied by Warner (1977) and Herrnkind (1969, 1975, 1983, 1985), none of the more or less controversial interpretations offered hitherto allows unequivocal understanding of the stimuli for this behaviour (see Text-fig. 6C).

In xiphosurans, seasonal migration from the open sea towards shallows to mate is known (see references in Caster 1938; Shuster 1950, 1960; Herrnkind 1983; Boucot 1990, p. 397; Speyer 1990) both in the U.S. Atlantic *Limulus polyphemus* Linnaeus and the Alaskan *Paralithodes camtschatica* Tilesius, the latter of which may even form 'pods' of juvenile and subadult specimens (Speyer 1990, p. 407). On the other hand, *Limulus polyphemus* living gregariously along the U.S. Atlantic shores are occasionally stranded ashore to form a kind of beach bar (see Shuster 1960).

In freshwater gammarid amphipods that live in isolated clusters, the migratory behaviour was recognized (Goedmakers and Pinkster 1981; Goedmakers 1981) as occasional, resulting from a necessity to feed and reproduce (for other interpretations see Goedmakers and Pinkster 1981).

In insects, there are the so-called *processionary caterpillars* whose behaviour is nearly identical to that of the above-described arthropods. This behaviour is found in some species of the order Lepidoptera (see

Scoble 1992, p. 331) and is well exemplified (see Prüffer 1954, Szujecki 1995; and Text-figs 6A-6B herein) by caterpillars of the moth *Thaumetopoea* (=*Cnethocampa*) *pinivora*, a severe pest of European pine forests, which appears abundantly in some years. The caterpillars migrate gregariously in July to September, foraging for fresh twigs of pine (or, according to some authors, wandering to moult) and moving in lined-up long queues, the members of which touch one another and spin out a cobweb-like thread to guide their way. Another species, *Thaumetopoea* (=*Cnethocampa*) *processionea* feeds on old oaks, and has a similar migratory behaviour.

AGGREGATION IN CAMBRIAN ARTHROPODS FROM CHINA

A mysterious and enigmatic case has quite recently been reported by Hou *at al.* (October 2008) from the Lower Cambrian of China. It concerns tiny phyllocarid ('*Waptia*-like') arthropods strung out in thread-like (? palolo-like) chains that locally bifurcate (see, right side of fig. 1B in Hou *et al.* 2008), these being interpreted by Hou *at al.* as formed by the telescoping of pelagic specimens, or their chains, when falling one upon (or, into) the other, more or less vertically to the sea bottom. The organization of these chains is more reminiscent of those resulting from asexual budding, typical of some present-day polychaetes (see Lemche 1957, Kielan 1958), than any aggregation in trilobites.

AGGREGATION IN PRESENT-DAY GASTROPODS

Structurally similar to the trilobite queues are some aggregations of gastropods. Such are the so-called *copulatory chains* formed temporarily by some hermaphroditic pulmonates, for instance by the common European freshwater snail *Ancylus fluviatilis* O.F. Müller, 1776, as illustrated by Geldiay (1956, fig. 1). Also well known are the obligatory sex-regulated stacks, or chains, of the protandric marine prosobranch species of the slipper-limpet genus *Crepidula* Lamarck, 1799, both present-day and Tertiary (see Bałuk and Radwański 1985). In such stacks, in their normal life mode of life (not in a copulatory position!), a dozen or so individuals perch on one another to keep the old females (often dead) at the base, younger females with inter-sexed individuals above, and dwarfish males on top (see, e.g., Coe 1936, figs 1–2; Boucot 1990, p. 398; Grant-Mackie 1990, figs 329–334).

THE CHARACTERISTICS OF THE TRILOBITE QUEUES

The trilobite queues, composed of almost completely preserved exoskeletons, represent *body clusters* as distinguished by Speyer and Brett (1985) and Speyer (1987, 1990), with no disarticulated exuvial debris found along, or around (see Pls 1–5). All the trilobites in the queues are preserved with their complete exoskeletons and show dorsum-upwards orientation.. This clearly indicates their burial in life position, that is, the live or freshly dead specimens have been frozen when queuing over the seafloor (sediment/water interface).

The majority of the queues are formed from the largest individuals. The smaller-sized individuals are arranged as a rule in short files consisting of only two individuals (see Pl. 1, Figs 1–3). In such 'immature' queues the trilobites are positioned either separate from one another (Pl. 1, Figs 1–2), or with an overlap (Pl. 1, Fig. 3)

In general, the queues are organized in single file, either almost straight or slightly twisted (Pl. 1, Fig. 6; Pl. 2, Fig. 4; Pl. 3, Fig. 2; Pl. 4, Fig. 1), and/or arched to a variable extent (Pl. 1, Fig. 7; Pl. 4, Fig. 2; Pl. 5, Figs 1–2), with all intermediate arrangements.

The highest number of trilobites in the queues actually collected is nine, eight of which are illustrated (Pl. 4, Fig. 2; the ninth being outside the upper margin of the photo). In some less compact marlstone slabs that completely broke into pieces during excavation, the greatest number of queuing trilobites was thirteen.

The individuals forming the queues are either positioned one-by-one, as if walking in Indian file, with no contact between them (e.g., Pl. 1, Figs 4b–4c; Pl. 2, Figs 1a–1b, 4b–4c, 6d–6e) or, more commonly, with 'head-to-tail' contact with a variable degree of overlap either by the cephalon, or by the pygidium. To describe the latter features, the terms *prosocline* and *opisthocline* are adopted, following the terminology used earlier (Seilacher 1970, p. 452; Orłowski *et al.* 1971, p. 346; Radwański 1973; Żylińska and Radwański 2008) for the bottom-ploughing/furrowing Upper Cambrian specimens. Thus, termed *prosocline* (=head-down; or, head-under-tail) are members whose cephalon is inclined below the pygidium of the member preceding it in the queue (e.g., Pl. 1, Figs 3b, 7b; Pl. 2, Fig. 5c; Pl. 4, Figs 1e, 1f; Pl. 5, Figs 1e, 1f, 2b), whereas *opisthocline* (=tail-down; or, head-upon-tail) are members whose cephalon oversteps the pygidium of the member in front (e.g., Pl. 1, Figs 6b, 6c; Pl. 2, Figs 3b, 4b, 4e, 6b, 6d). Some prosocline specimens, when overlapped by an opisthocline one, may be distinguished as *isocline* (e.g., Pl. 4, Fig. 2b; Pl. 5, Fig. 1c).

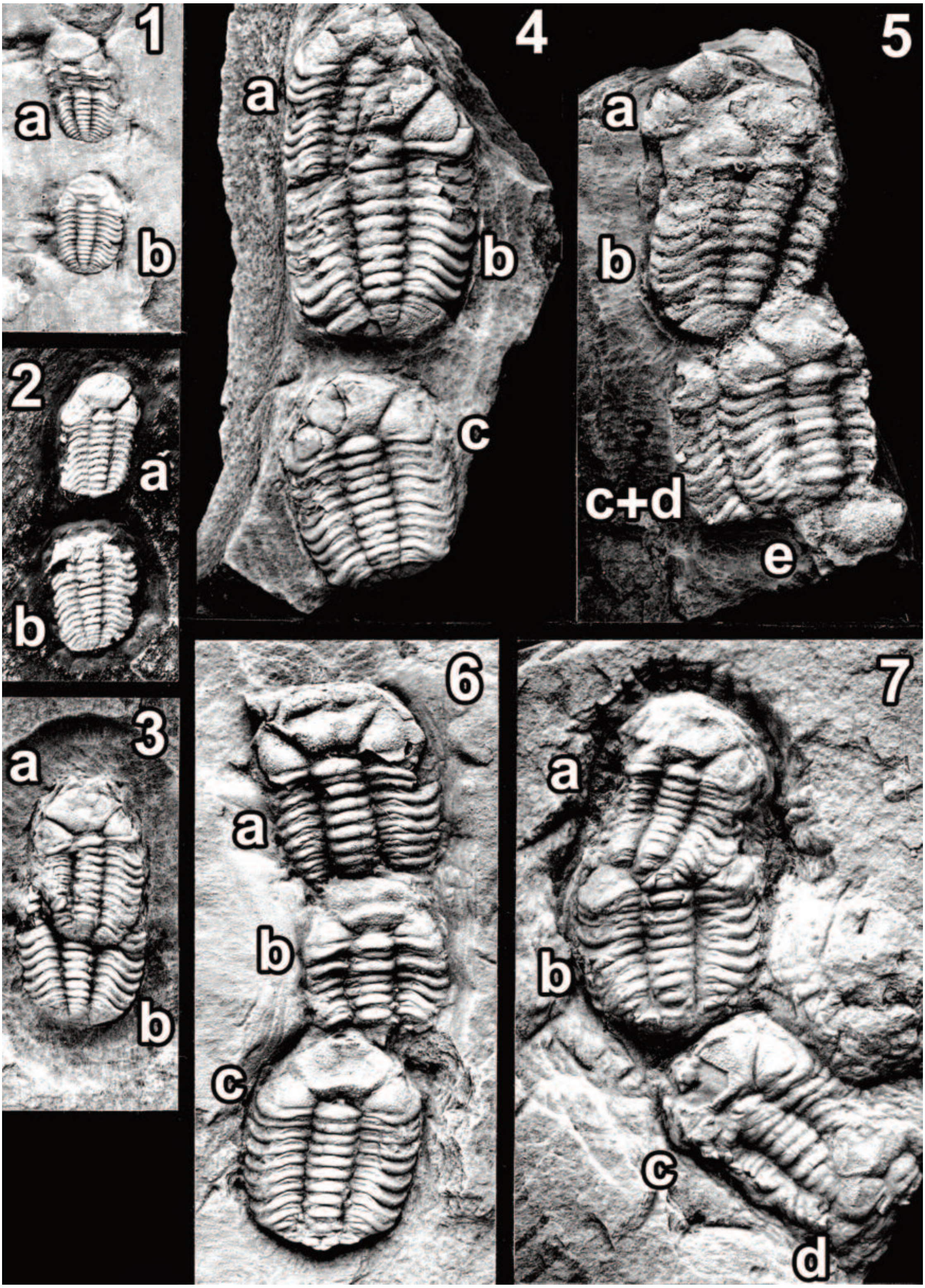


Plate 1. Early Famennian *Trimerocephalus* queues from the Holy Cross Mountains. Shorter queues composed of up to five individuals: **1-3** – Smaller-sized individuals, **4-7** – Average-sized individuals; all × 3, further explanation in the text

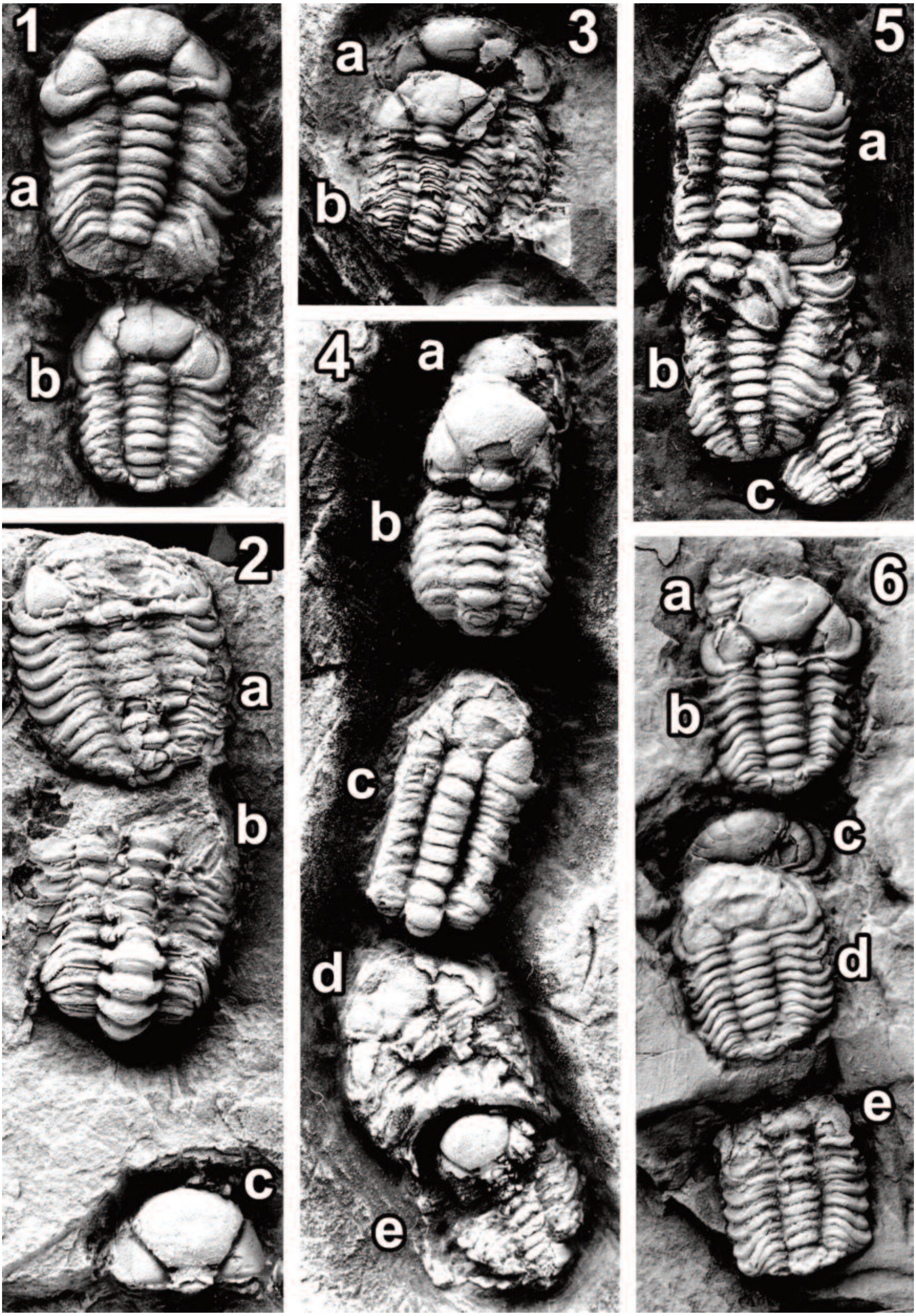


Plate 2. Early Famennian *Trimerocephalus* queues from the Holy Cross Mountains. Variations in position and preservation of individuals within queues of shorter or longer extent; all × 3, further explanation in the text

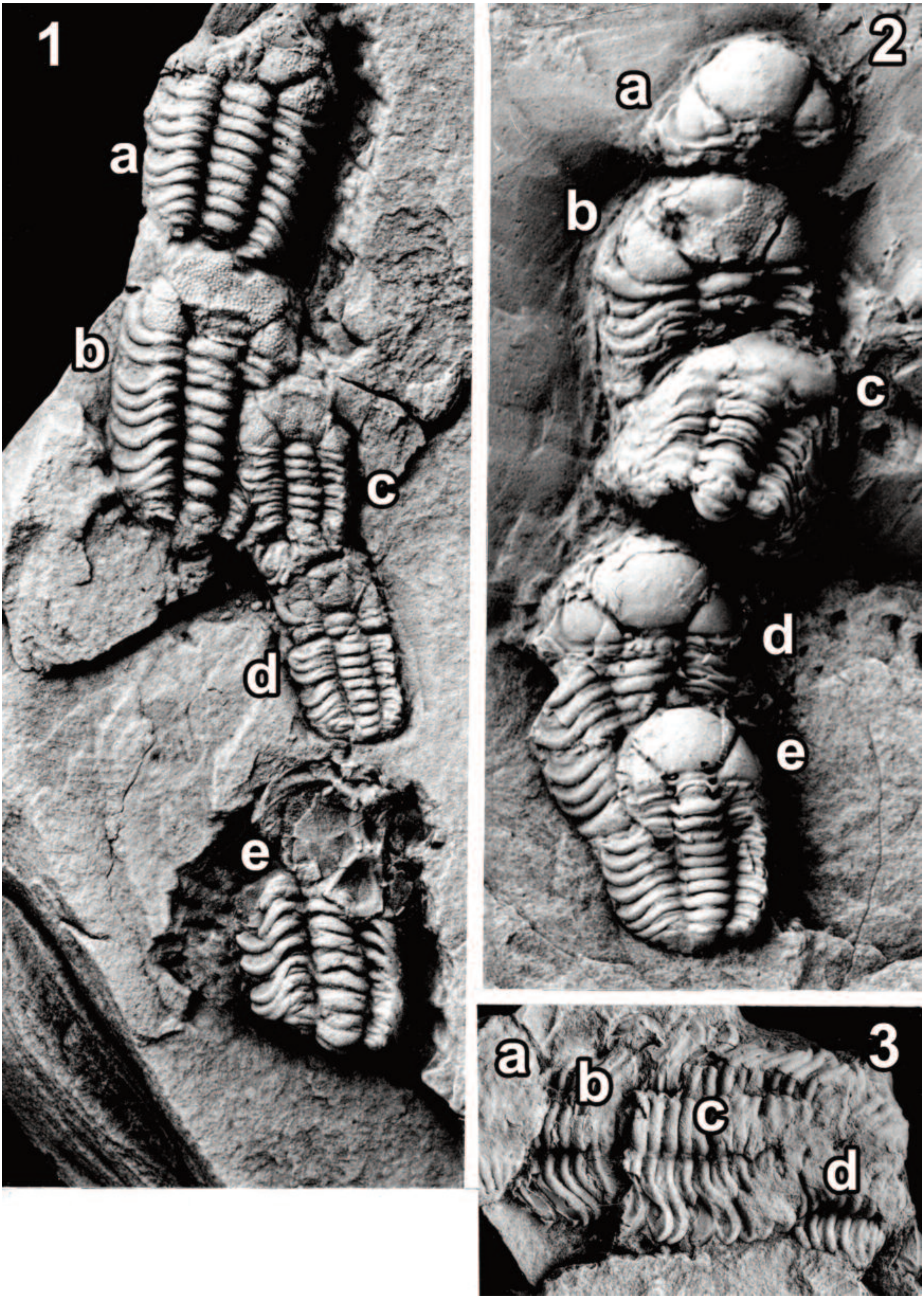


Plate 3. Early Famennian *Trimerocephalus* queues from the Holy Cross Mountains. Variations in the structure of longer queues: **1** – Slightly disarrayed queue, **2** – Queue of individuals oriented head-upon-tail (opisthocline), **3** – Jam of four individuals stacked one upon the other; all × 3, further explanation in the text

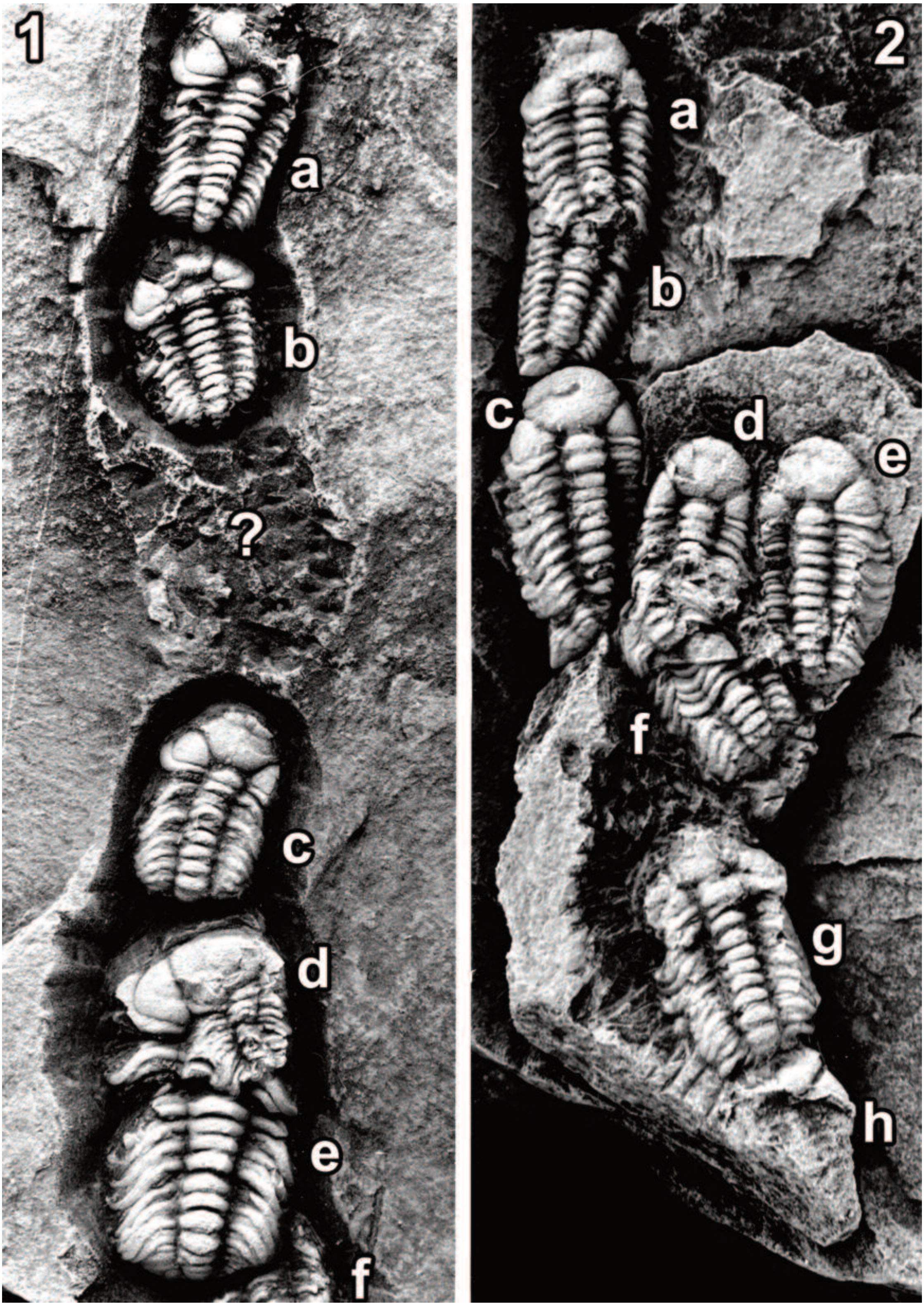


Plate 4. Early Famennian *Trimerocephalus* queues from the Holy Cross Mountains. Variations in the structure of longer queues: **1 –** Queue with one member absent, **2 –** Queue with a jam of three individuals to one side of the main file; all × 3, further explanation in the text

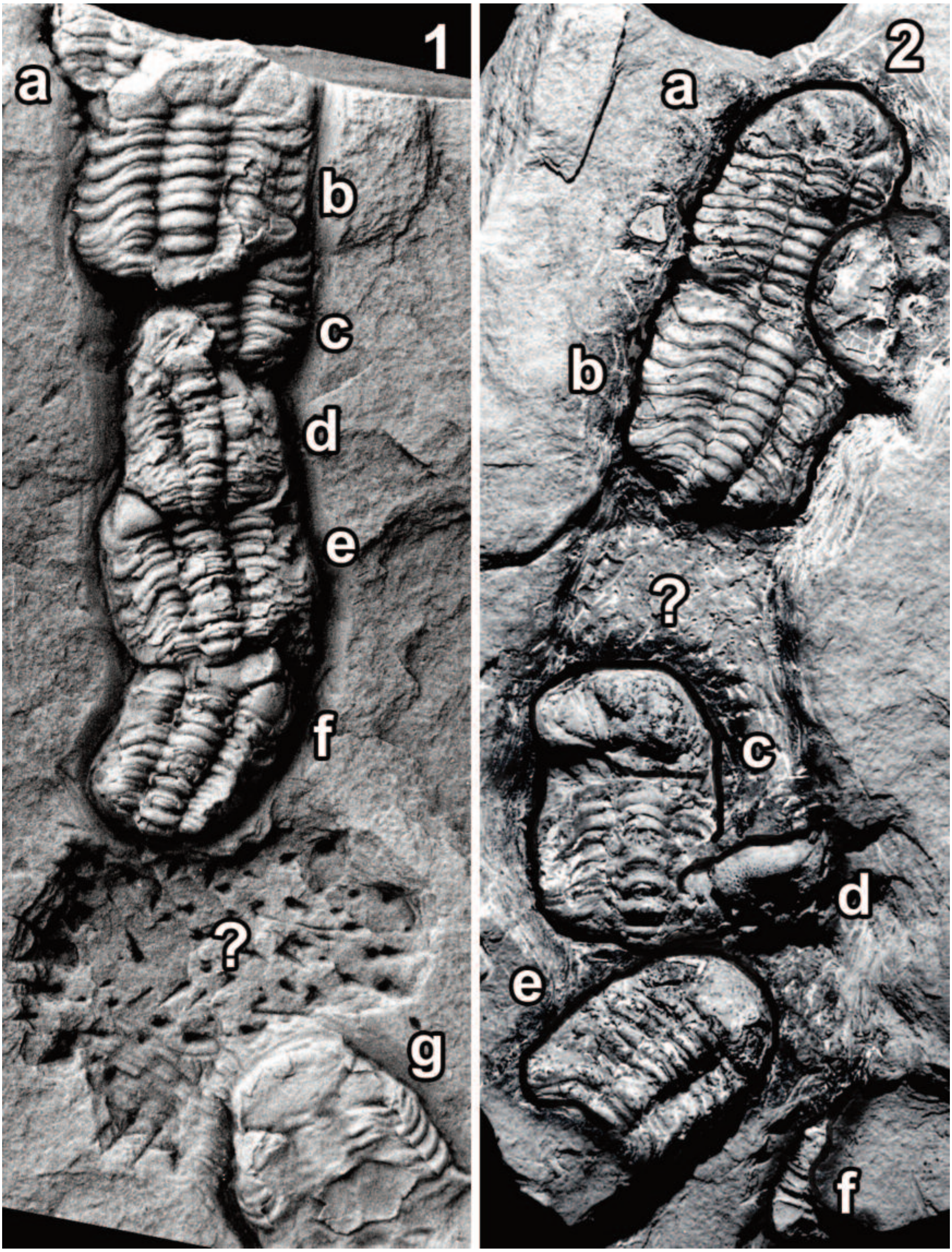
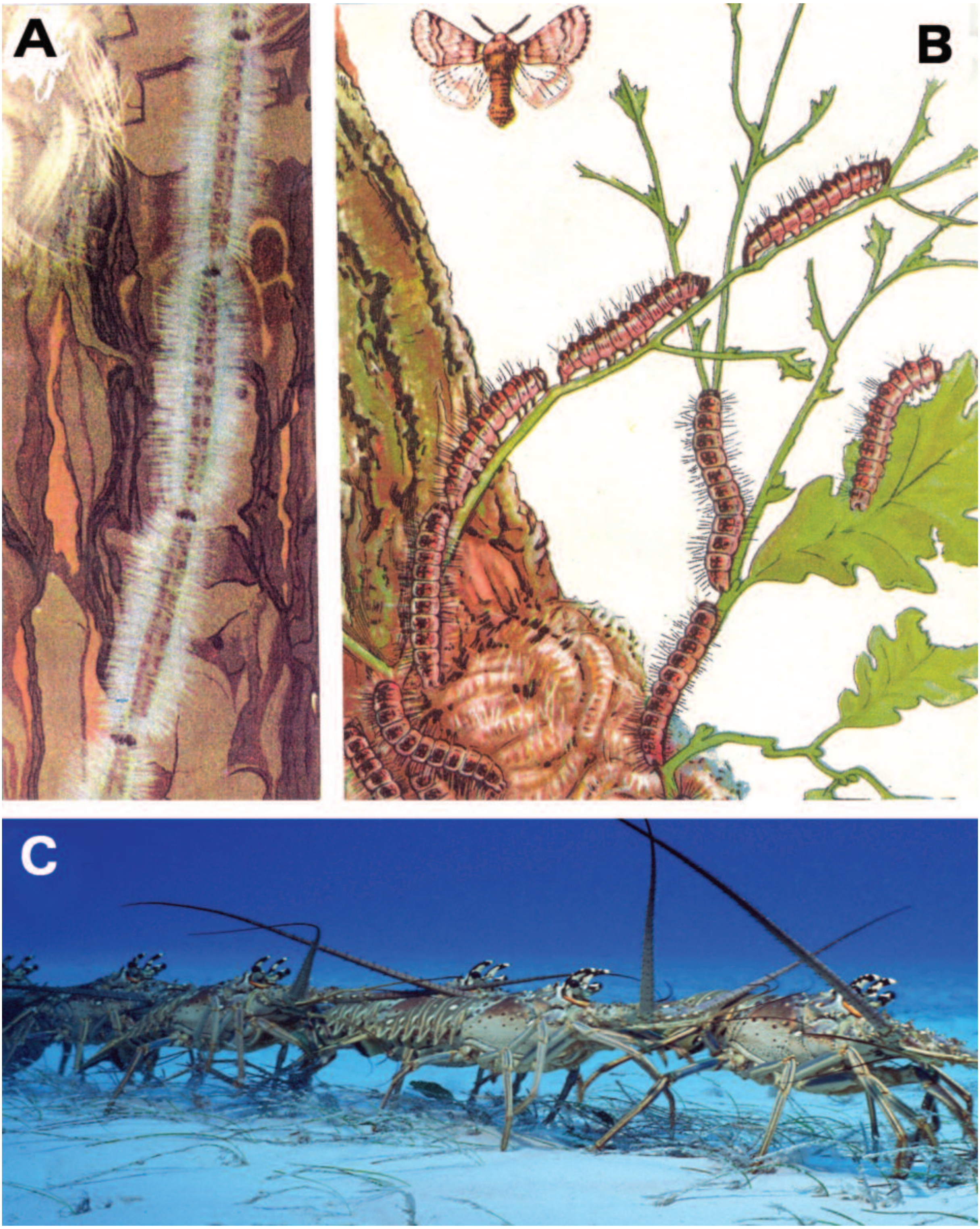


Plate 5. Early Famennian *Trimerocephalus* queues from the Holy Cross Mountains. Variations in the structure of longer queues: **1 –** Queue with most individuals oriented head-under-tail (prosocline), but one missing; Collection of Dr. T. Ochmański; **2** – Queue with a jam of two individuals disarrayed from the file, and with a vacant place for a missing individual; all × 3, further explanation in the text



Text-fig. 6. Examples of migratory behaviour in present-day arthropods. **A**, **B** – The processionary caterpillars, known from European forests: A – *Thaumetopoea pinivora* on the trunk of a pine (adapted from Heintze and Zdzitowiecka 1963, p. 53), B – *Thaumetopoea processionea* on twigs of an oak (adapted from Szujecki 1995, fig. 8.145; after Prüffer 1954), **C** – Migratory behaviour of the present-day Spiny Lobster, *Panulirus argus* (Linnaeus): A fragment of the larger queue, similar to that photographed by Herrnkind (1975, p. 828) off Bimini, Bahamas

Some members overlapping one another in the queue look as if they moved forward unexpectedly, to form a heap (Pl. 2, Figs 5a–5c), while others were left behind slightly (Pl. 1, Fig. 4c; Pl. 2, Fig. 2c). On the other hand, there also appear to be local jams full of several individuals. In such jams, some individuals are positioned either on top of the others (Pl. 2, Figs 5a–5b), or to one side of the main course of the queue (Pl. 4, Figs 2d–2f). Another type of local jam (Pl. 5, Fig. 2) is thought to have resulted from two individuals (2d and 2e) fighting to get a place in the queue.

In some queues, a tegular arrangement is seen, in which all the members overlap in an opisthocline mode (Pl. 3, Fig. 2); in other queues prosocline members are frequent (Pl. 5, Figs 1e–1f).

Within the queues, some members may overlap one another almost completely (Pl. 1, Figs 4a–4b, 5c–5d; Pl. 2, Figs 3a–3b, 4a–4b, 6a–6b, 6c–6d), even locally forming stacks composed of several individuals (Pl. 3, Figs 3a–3d; Pl. 5, Figs 1a–1c).

In the case of two individuals in contact, their position (opisthocline) where the succeeding queue member overlaps the preceding one (e.g., Pl. 2, Figs 3a–3b) is identical to that of the mating position of a pair of modern horseshoe crabs in nuptial embrance (see Caster 1938, figs 4a–4b; Shuster 1960, fig. in p. 6; Hu 1971, fig. 5); however, the copulatory posture in trilobites is poorly known and very variable (Hu 1971, pp. 122–124). If the queues formed for mating, they should preferably be composed of opisthocline couples and/or groups. Amazingly, in some well-organized (‘well-ordered’) queues, one place in the file is free, lacking a member (see Pl. 4, Fig. 1, between members 1b and 1c; Pl. 5, Fig. 1, between members 1f and 1g; Pl. 5, Fig. 2, between members 2b and 2c); this peculiar feature is interpreted later in the paper. The smaller breaks in the continuity of the queue, where the successive members are positioned half a body length apart or less (see Text-fig. 3), may correspond to the length of antennae through which these members could make contact.

Apart from the physical contact (through antennae and/or legs; see Herrnkind 1969, 1975), chemosensory reception of the blind trilobites, either by pheromones or urine dispersal (see Atema 1995) may be taken into account. The biochemical stimuli of various invertebrates enable differentiation between conspecific individuals and strangers (e.g. predators; see Snyder and Snyder 1970, Lawrence 1991, Aronson and Blake 2001). On the other hand, as stated in the present-day lobsters (Atema 1995), social behaviour depends greatly on chemical signals.

In any case, the lack of vision in the blind trilobites did not necessarily affect their ability to form queues. As shown in experiments by Herrnkind (1969, p. 1426), Spiny Lobsters blinded by eye-tagging were readily able to form queues in exactly the same way as non-blinded individuals.

All the trilobite queues display the effect of the presumed mortal spasm, which caused particular members of the queues to become disarrayed from the ideal ‘head-to-tail’ contact. It is thought that the individuals with a higher life potential were able to move blindly onwards along, or beside the queue, when the preceding queue member was already torpid or dead. This may explain both the variable overlap of particular individuals, as well as the formation of local jams.

FORMATION OF THE QUEUES

From the above reviews on aggregation in present-day arthropods, it is apparent that the migratory aggregation of the trilobites in this study is evidently of a behavioural nature. The general cue triggering their migration was not a biological stimulus in search for food, moulting, or mating, but environmental stress. The latter is evident from a report by Herrnkind (1975, p. 829) that a group of Spiny Lobsters reared in a vinyl pool had marched around it day and night for two weeks. The queuing was also recognized as triggered by an increased water motion, storm action, or seasonal (autumnal) temperature drop (Herrnkind 1969, 1983). Environmental stress, caused by any fluctuation of physical or chemical parameters, has always been noted as dramatic for all stenotopic biota. It has its most extreme effect in shallow to extremely shallow seas, where it is often manifested by mass-mortality events (see Glynn 1968, Hendler 1977, Smith 1984, Lawrence 1996).

The mode of preservation of the queues, as well as the lithology of the ambient sediment (Unit I), strongly suggest that such conditions obtained when the trilobite-bearing sequence of Kowala was formed. This sequence, regarded as of deep-water basinal facies (Szulczewski 1971, fig. 11, and 1995; Berkowski 2002), bears its Unit I, which besides the trilobites studied herein, is unfossiliferous. It is thought that the queues originated at a time of shallowing of the basin. The most probable event is an extreme shallowing which dramatically induced not only environmental stress for the trilobites and their resultant queuing, but also created conditions guaranteeing their preservation.

It is noteworthy that, in present-day marine arthropods, aggregations of any kind have been noted only from shallow water, namely in crabs (see Warner 1977) spiny lobsters (e,g, after Hurricane Betsy in 1965; see

Herrnkind 1975, p. 830) and king crabs (see Shuster 1950, p. 20; 1960).

In shallow marine environments, one of the most dangerous factors is exposure to the air, which occurs primarily at extreme ebb tides. How the vagile benthic animals then react, is clearly shown by their emergence from burrows. Such a mass emergence of the shallow-burrowing echinoid *Echinocardium cordatum* (Pennant, 1777) onto the intertidal flat was reported by Higgins (1974, p. 470 and Pl. 7*b*) from Matakatea Harbour in New Zealand. This was caused, according to Higgins, by a combination of a high air temperature, very sunny conditions, and a particularly low tide during the warmest hours of the day. All these factors, acting together, had driven the echinoids to try to escape from their burrows. The presumed resultant overwarming, beyond the temperature at which the animals could survive, has subsequently been recognized (see Smith 1984, p. 15 with references therein; Radwańska 1999b, p. 357) as a lethal agent for the echinoids. Moreover, exposure to the air is itself potentially fatal to echinoids, which can then survive not more than two or three hours (Smith 1984, p. 15).

The interpretation that similar conditions of overwarming and/or drought, combined with a possible salinity shock (regardless of its trend, oligo-, or hyper-; cf. Smith 1984, p. 15), created lethal conditions for the trilobites aggregating in queues when exposed at very low water at Kowala is thus highly plausible

With the water column diminished to a thin film, the surface tension on water became an entrapping agent that adhered any creature firmly to the sediment surface. In other words, in such circumstances the sediment/water interface had reached sea level, and any creature on the sediment surface had to break out of the water film, thus becoming exposed to the air. This is thought to have effectively killed the trilobites, which suffocated and desiccated in the positions they kept when lined up in a queue.

If we locate the trilobite queues on a vast inter- or peritidal flat, then a still more substantial problem arises concerning the time and nature of their covering (burial) by the incoming sediment.

Under intertidal conditions, the breakdown of corpses progresses fast. Both the gases arising from the decay, and the air that enters the suffocated and/or desiccated bodies, cause them to float when the water returns, as observed in present-day crabs (see Speyer 1987, pp. 216–217) and echinoids (see Smith 1984, p. 15), as well as in experiments with killed stomatopods (Hof and Briggs 1997, p. 423). It is thus apparent that the burial of the queues had to be both very rapid and take place under hydrodynamically extremely quiet conditions. Anyway, if the trilobites were already dead, their corpses had to be firmly anchored/adhered to the sediment surface if they were not to become buoyant when covered with water again.

The firm adherence of the queues to the sediment surface (coincident with the sediment/water interface) resulted from the cohesion due to desiccation and from the surface tension on water when the trilobites were lifeless and more or less desiccated. This ensured their entrainment in place until covered by the incoming sediment, and prevented them from floating at the first rise in water level of a renewed highstand (? high tide).

A peculiar feature of some of the trilobite queues is the absence of one individual from the queue (see Pl. 4, Fig. 1 and Pl. 5, Figs 1–2). This is interpreted as reflecting the survival of some individuals that, managing to avoid suffocation/desiccation, were still alive and thus capable of escaping from the queue; their departure as the water level fell rapidly having saved their lives (!).

Furthermore, the specimens positioned more or less completely one upon the other are thought to represent living individuals that were able to clamber onto or walk upon individuals that were already dead.

BURIAL OF THE QUEUES

To determine the time of burial of the queues, some data on the taphonomy of present-day crustaceans are taken into account. Such limited reports primarily concern crabs and shrimps (see review by Bishop 1986, and Feldmann *et al.* 1999), and stomatopods (see Hof and Briggs 1997, Stankiewicz *et al.* 1998). In these crustaceans, cuticle decomposition in shrimp corpses proceeds usually in a few days (Bishop 1986, p. 329), and in stomatopods in a few weeks (Stankiewicz *et al.* 1998). Similar data on the decomposition of soft tissue and disintegration of skeletons are available for many invertebrates, as exemplified by echinoids, primarily those having their spine canopy preserved intact (see review by Radwańska 1999b, Radwański and Wysocka 2001, 2004). In echinoids, the epithelium of individuals kept under quiet conditions in aquaria decomposes in several days after death, resulting in the total denudation of their spines (in 5 to 9 days, as observed by David Nichols, in Aslin 1968).

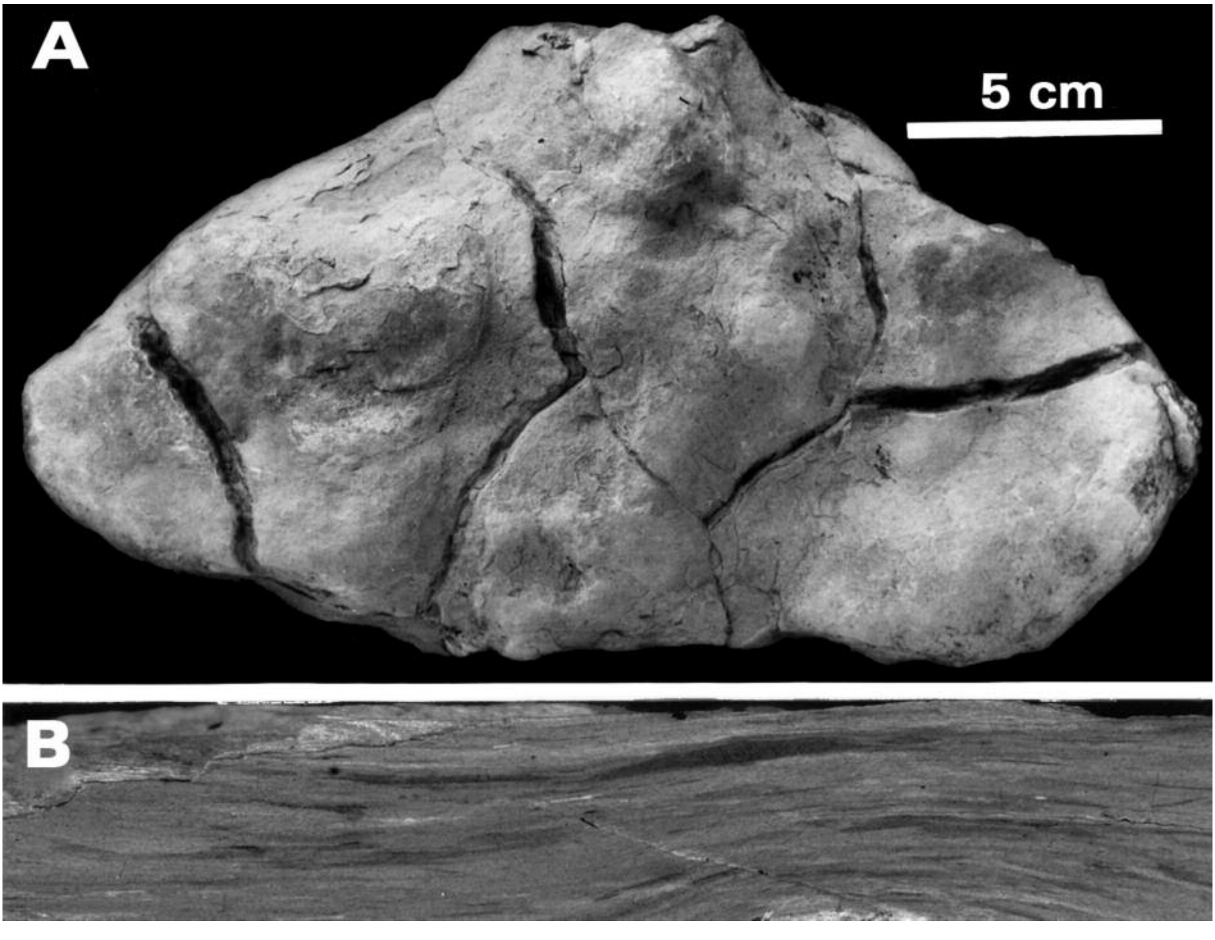
Considering that the decomposition of present-day crustacean corpses progresses so fast, it can be inferred on uniformitarian principles that the preservation of the trilobite queues in their original array, and with the exoskeletons intact, evidences their burial very soon after (‘almost simultaneously’) the queues were organized.

Such burial could not happen under deep water conditions where the sedimentation rate is low, and any animal remains have no chance of remaining on the seafloor for any length of time, being exposed to the action of various factors, both biogenic (scavengers) and physical (waves and/or currents, mass movement).

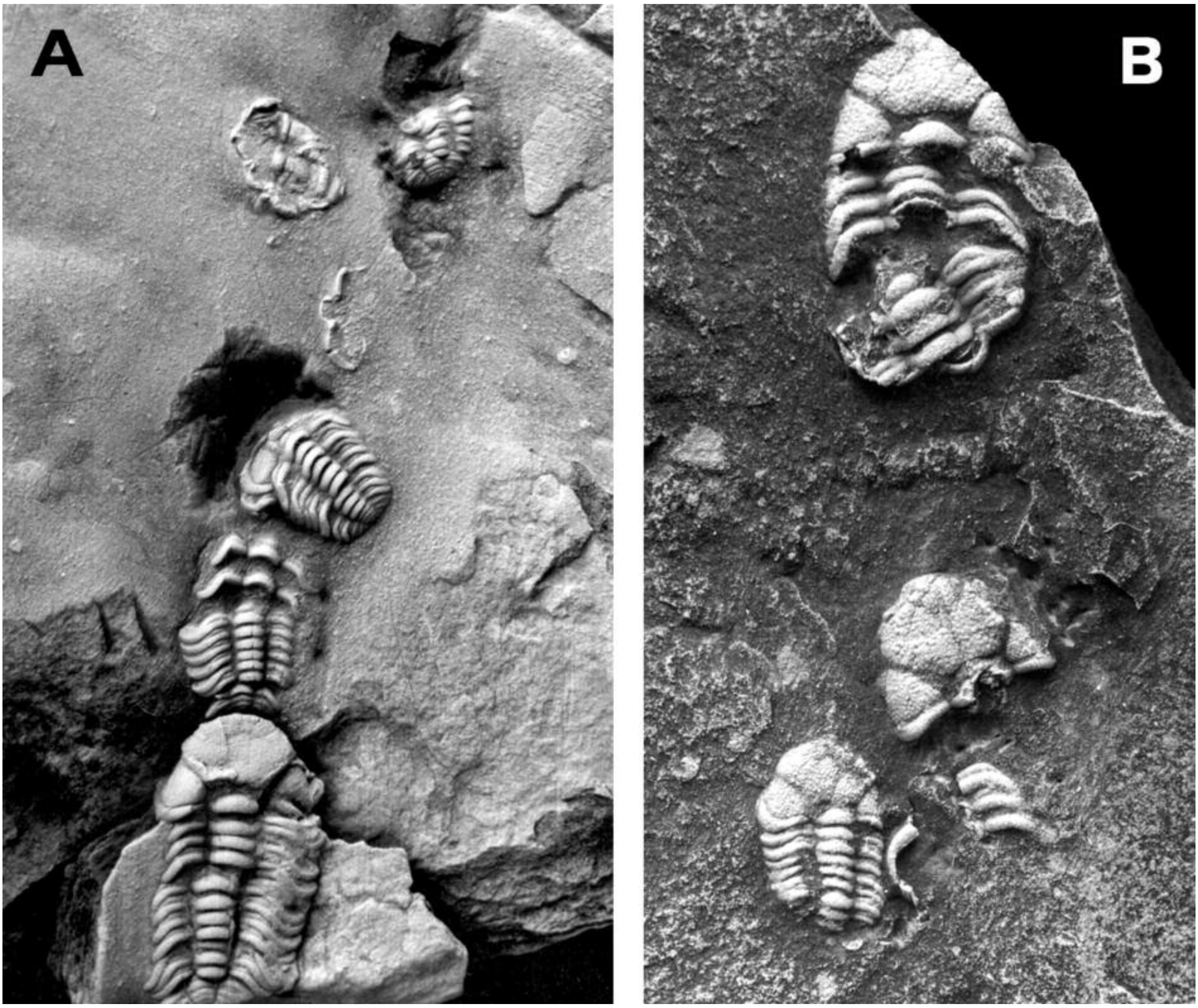
The delicate lamination of the marlstones that yield the trilobite queues, and the fact that the queues did not become disarrayed, both indicate a very slow, quiet but continuous rise in water level progressively inundating the queues. Flocculation of the suspended marly ooze could then have been the primary agent producing the sediment that entombed the frozen queues. A very mild motion of water sweeping the bottom produced a microlenticular lamination structured like a microflaser stratification, but it was too weak to disarray the queues, which adhered firmly to the sediment surface.

A microflaser stratification (see Text-fig. 7B) of fine-particle sediment originates from polydirectional movement of water. It is thus produced either by the most distal turbidity currents, usually at deeper depths, as well as by mud-loaded waters in tidal ponds, lagoons, or lakes of various kind, including deserted playas (see Grande 1984, fig. I.3). Of these environments, tidal/peritidal flats are the most probable.

Additional palaeoecological information is provided by the structure of the calcareous nodules. These synsedimentary nodules were formed at or just below the sediment/water interface and were most probably at least partially exposed exposed above the seafloor, as indicated by some badly organized trilobite queues that look as if the trilobites were walking, or crawling upon them, especially along their circumference (see Text-fig. 3). It should be noted that conodonts are commonly present in the nodules, which clearly acted as sedimentary or preservational traps, whereas in the adjacent marlstone the conodont frequency is very low or nil (Professor Dr. Zdzisław Bełka, personal information). Some of the nodules are superficially cracked over their upper side (see Text-fig. 7A). The cracks might have been formed either underwater by synaeresis, or by desiccation when the nodules were exposed to air. Considering that



Text-fig. 7. Sedimentary structures of the trilobite queue-bearing Horizon 1 (arrowed in Text-fig. 2B): **A** – Mud-cracked calcareous nodule, **B** – Microflaser stratification of the ambient marlstone



Text-fig. 8. Two examples of disarranged trilobite queues from the topmost part of the queue-bearing Horizon 2 (arrowed in Text-fig. 2B): an effect of progressive decay and/or water motion at a highstand when sedimentation discontinued (? a long-term omission surface, see the text)

synaeresis typically affects the entire sedimentary body (a layer, or a nodule), and desiccation only the part exposed to the drying factor (e.g., sunlight), the observed structure indicates desiccation cracks in nodules exposed to the air at extreme low water.

To sum up, it is reasonable to infer that the trilobite queues were preserved on a surface on which sedimentation had totally ceased and from which the water column had disappeared. When sedimentation recommenced as the water rose, the desiccated queues, firmly attached to the substrate, become quietly blanketed by mud, and finally entombed. In the uppermost part of the Second Queue-bearing Horizon (2 in Text-fig. 2B), the queues were not so stable (see Text-fig. 8) and, either when a high stand progressed the water motion disturbed them reasonably, or decay processes (see Hof and Briggs 1997, fig. 1D) caused their disarrangement during a break in sedimentation.

The appearance of such disorganized queues (Text-fig. 8) is nearly identical with a linear cluster figured by Slavičkova and Kocourek (2000, fig. 1a–b) of the odontopleurid trilobite *Leonapsis leonhardi* (Barrande, 1846) from the Silurian of Bohemia, and interpreted as current-arranged (Slavičkova and Kocourek 2000, p. 156; Chatterton *et al.* 2003, p. 170).

CONCLUDING REMARKS

The most suggestive scenario of successive events to create the queues of blind trilobites, assigned tentatively to the species *Trimerocephalus mastophthalmus* (Reinhard Richter, 1856), seems to have been set within a part of the Upper Devonian basin of the Holy Cross region tending temporarily, or intermittently, to upheaval in Early Famennian time. Regardless of the poor, or virtually non-existent record of other benthic animals, the area of Unit I of Kowala had to be populated by creatures (? all soft-bodied) that became, or produced, food for these trilobites. Of skeletal animals, the blind trilobites constituted an opportunistic species, well adapted to successfully colonize extremely shallow, muddy/calcareous, possibly turbid and semi- or non-translucent waters. Under such conditions, the selection pressure by predators, significant in other habitats (cf. Clarkson 1967, Aronson and Blake 2001), was minimal or none, and this guaranteed security for the gregariously living trilobites. During the development of Unit I of Kowala the conditions favouring preservation of the trilobite queues appeared only twice, just at the time when the extreme shallowing of the basin was established. This was fatal for the majority of the trilobites, which lost their lives at drought when they tried to migrate in queues in order to escape from the hostile environment.

As a mortal agent for the queues desiccation is assumed. Although a few individuals (the missing members in longer queues, see Pl. 4, Fig. 1 and Pl. 5, Figs 1–2) were able to escape from the cataclysm, the others became entrapped by the surface tension, and glued in their death throes to the sediment surface. The queues thus represent both a frozen behaviour *sensu* Boucot (1990), and a mass-mortality bioevent of Feldmann and *al.* (1999). On the other hand, all members of the queues are preserved *in situ*, in *life position* generally, but specifically in their death throes. This largely extends not only the previously known records of frozen behaviour in trilobites (see Text-figs 4–5), but also the number of trilobite aggregations of any kind so concisely surveyed by Speyer (1990, Table 32) and supplemented by subsequent authors (Fortey and Owens 1999, Suzuki and Bergström 1999, Davis *et al.* 2001, Chatterton *et al*. 2003, Chatterton and Fortey 2008, Gutiérrez-Marco *et al.* 2009).

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