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ABSTRACT

Dikelocephalus is well-represented in Upper Sunwaptan (Upper Cambrian) deposits throughout the northern Mississippi Valley. Neglect of the preservational, biostratinomic and functional aspects of *Dikelocephalus* has prohibited comprehensive systematic study of the genus to date. Taphonomic artifacts have been mistaken for characters of taxonomic importance. In order to provide a basis for 1. revision of the systematics of the genus, and 2. examination of patterns of variation within a geologically well constrained Cambrian trilobite, taphonomic and functional aspects of *Dikelocephalus* are assessed. Data from extensive new collections indicate that transport of *Dikelocephalus* sclerites away from the life habitat has been minimal. Functional and geological evidence suggest that *Dikelocephalus* was epibenthic. Morphological variation within the genus cannot be directly related to paleoenvironment. Identification of these functional and taphonomic controls on *Dikelocephalus* will permit detailed analysis of species-level variation within the genus.

INTRODUCTION

The paleobiology of Cambrian species is poorly understood. Trilobites, which are anatomically complex and occur in large numbers, provide the best opportunity for examination of patterns of variation within Cambrian species. However, most studies of Cambrian trilobites are descriptions of new faunas with scant attention to taphonomy, intra-specific variation and functional morphology. A series of papers on the paleobiology of uppermost Cambrian trilobite *Dikelocephalus* and its geological setting (Labandeira, 1983b; Hesselbo, 1987b; Hughes, 1988, 1991a,b, 1992) aim to provide the first comprehensive documentation of patterns of variation within Cambrian trilobite species. The data on distribution, preservation and paleoecology included in this paper are essential to appreciate the unusually high level of intra-specific developmental flexibility within *Dikelocephalus* (Hughes, 1990; 1991a). They have also been fundamental in establishing the basis for taxonomic revision of both the genus and the entire dikelocephalid clade.

DISTRIBUTION

Dikelocephalus is found in Upper Sunwaptan (Ludvigsen and Westrop, 1985) deposits from the North American craton (Taylor, 1977; Hughes, 1990; 1991a, Hughes and Rushton, 1990). The Upper Sunwaptan is equivalent to the Trempealeaun Stage, as previously defined in the northern Mississippi Valley (Nelson, 1956). *Dikelocephalus* only occurs in large numbers in the northern Mississippi Valley (central/western Wisconsin, southeastern Minnesota, and northeastern Iowa; Figs. 1 and 2). Within the northern Mississippi Valley it occurs the Tunnel City Group (Ostrom, 1966, including in both the Reno Member and the Mazomanie Formation; Fig. 1) and in the overlying St Lawrence and Jordan Formations (Fig. 2). Appendix 1 is a list of localities within the northern Mississippi Valley from which *Dikelocephalus* has been collected.

Along with the trilobite *Illaenurus priscus*, the first occurrence of *Dikelocephalus* defines the base of the Upper Sunwaptan in the northern Mississippi Valley. *Dikelocephalus* is most abundant in the St Lawrence Formation, within which it is common in heterolithic beds (comprised of centimetre-scale interbeds of very fine sand and dolomite-rich clays), rare within laminated sandstones, and has not been recorded in stromatolitic dolomite (Hughes, 1990). Scattered outcrops of the St Lawrence Formation occur in a belt running between Minneapolis/St Paul, Minnesota and Madison, Wisconsin (Fig 2.). The northwest/southeast trend of the outcrop belt approximately parallels paleoshoreline and provides an excellent opportunity to examine small scale patterns of spatial variation within the genus. The youngest known *Dikelocephalus* are two specimens from the Van Oser Member of the Jordan Formation (Pl. 1 Figs. 1,2).

PRESERVATION AND TAPHONOMY

Preservation of individual sclerites

Preservation of the cuticle is extremely rare. Only three specimens (out of approximately 2750) from the northern Mississippi Valley display partial preservation of the original cuticle of *Dikelocephalus* (Pl. 1, Figs. 1-4). Measurements from thin sections of sclerite fragments indicate that *Dikelocephalus* cuticle varied in thickness from at least 50 to 125μm (Pl. 1, Fig. 5). Similar values are common in many other trilobites (Dalingwater, 1973). Although the cuticle of *Dikelocephalus* was probably thinner than that of some late Paleozoic forms (*e.g. Phacops*, in Miller and Clarkson, 1980), it was not unusually thin, as in some Cambrian trilobites (Jell, 1978). Almost all specimens of *Dikelocephalus* from the northern Mississippi Valley are composite-molds (*sensu* Bambach, 1973; Pl. 1, Fig. 6) as is typical of trilobites preserved in siliciclastic deposits (Speyer and Brett, 1986). Diagenesis has usually destroyed the primary fabric of the matrix but detailed preservation of *Dikelocephalus* surface ornament in heterolithic beds indicates that the grain size of the primary matrix was very small.

Many trilobites show significant differences in the structure of the internal and external surfaces of the cuticle, particularly in the nature of surface ornamentation (Miller, 1976). These differences result in taxonomic complications when comparing northern Mississippi Valley trilobites with those from carbonate platform environments (Taylor, 1978) and they must be considered when discussing variation within *Dikelocephalus*. Surface ornamentation in *Dikelocephalus* includes terrace ridges and pustules (*sensu* Miller, 1976).

Terrace ridges, common in many trilobites, are thought to be confined to the external surface of the cuticle (Miller, 1975; Schmalfuss, 1978b; 1981). If this were the case they should appear only on the external mold. *Dikelocephalus*, however, shows terraces on the external and internal molds of both the dorsal surface and the doublure. During diagenesis, features of the external surface can be transferred or impressed onto the internal surface (Bambach, 1973; Rex and Chaloner, 1983; Rex, 1986). However the limited material of *Dikelocephalus* preserved with the original cuticle suggests that terraces were expressed on the internal and external surfaces of both the dorsal surface and the doublure (Pl. 1, Figs 2-4). Internal terracing is also present in specimens of the closely-related dikelocephalid *Briscoia sinclairensis* (Walcott, 1924, pl. 20 fig. 4) from limestones preserved without dissolution or compaction. Terracing on both surfaces is a primary feature of *B. sinclairensis*. All the evidence suggests that *Dikelocephalus* was terraced on both surfaces.

As the original cuticle of *Dikelocephalus* is poorly preserved the term 'pustulation' is used for all tuberculate features (following Miller, 1976). Uncompacted material of the Dikelocephalacea shows pustules in similar internal and external relief (*e.g. Saukia* in Westrop, 1986a pl. 3, fig. 12; ?*Prosaukia* in Shergold, 1975 pl. 15, fig. 3). These structures represent bulging of the cuticle and are referred to as domes (Miller, 1976, p. 342). Pustule size and distribution is identical on both internal and external molds of *Dikelocephalus* from the heterolithic facies and may represent domes (Pl. 1, Figs. 7,8). However, it could also be the result of diagenetic overprinting of exterior features on the internal surface.

Because cuticle thicknesses are negligible relative to the size of adult *Dikelocephalus*, either the internal or external mold can be used for morphometric study without adjustment for original sclerite thickness.

Deformation

Most specimens of *Dikelocephalus* are preserved without noticeable distortion of their original shape. Some, however, show post-burial deformation which includes cracking (e.g. Pl. 1, Fig. 9; Pl. 2, Fig. 2) and plastic flattening (Pl. 2, Fig. 1). Consideration of the mode and degree of deformation is essential before the paleobiology of *Dikelocephalus* can be assessed.

1. Effect of lithology on compression of fossils

The grain size of the sediment has a marked effect on the style of preservation. Sandstones preserve original shape (Pl. 2, Figs. 3-4), but are too coarse to preserve fine details of surface ornamentation (*cf.* Rex and Chaloner, 1983). Fine-grained units from fine-grained heterolithic beds often preserve surface ornament (*e.g.* Pl. 1, Figs. 7-8), but are subject to greater compaction (Ulrich and Resser, 1930).

2. Deformation within fine grained layers: cracking

The common occurrence of cracks in the cuticle indicates that most sclerites were rigid during compaction. Cracking is most frequent in large specimens. Aglaspidids from the same beds also show more cracking in large specimens than in small ones (Hesselbo, 1987a). Mechanical simulations of the formation of plant compression fossils suggest that the relationship between the size of the fossil and the compressibility of the sediment determines the amount of deformation. Smaller fossils are subject to less distortion than larger ones (Rex and Chaloner, 1983). Relative mechanical strength may vary with size and consequent changes in shape.

Patterns of crack development in *Dikelocephalus* are quite variable but comparison with uncompacted material shows that cracks are mostly confined to convex areas of the exoskeleton and are particularly common where steeply sloping surfaces intersect flat-lying ones (*e.g.* about the axial furrow; Pl. 1, Fig. 9; Pl. 2, Fig. 2). In such cases compression takes place in the vertical dimension and has caused little, if any, lateral expansion (Briggs and Williams, 1981; Rex and Chaloner, 1983).

A crack has developed in some specimens along the sagittal axis running anteriorly from the posterior margin of the occipital lobe across the first glabellar lobe (Pl. 1, Fig. 9). This crack is related to the break of slope at the sagittal line, along which compactional stresses have focused. The opening of this crack caused some lateral expansion in the transverse dimension (*cf.* Rex, 1986). A similar crack was noted in the olenid *Bienvillia*, preserved in fine-grained black limestones and shales, where flattening has distorted the cranidial morphology considerably (Fortey, 1974). In fine-grained units of the heterolithic facies, very large glabellae may show the development of irregular polygonal extension cracks (Pl. 1, Fig. 9). These may have been caused by the diapiric movement of mud upwards into the glabellar cavity.

3. Deformation within fine-grained layers: plastic flattening

Some specimens show evidence of plastic deformation. Large specimens from Arcadia (AAa, Bed 18, see Appendix 1) are flattened but are not cracked (Pl. 2, Fig. 1). Original convexity has been reduced; glabellar furrows and surface ornament are effaced. In contrast, most small specimens from the same horizon are slightly fractured and show no evidence of plastic deformation (Pl. 2, Fig. 2).

The cuticle probably became flexible in two stages. The initial decay of the organic framework caused the cuticle to weaken (Müller, 1979; Brett and Baird, 1986; Allison, 1986). This was followed by dissolution of the skeletal calcite, leaving a composite-mold which then deformed due to overburden pressure. Uniform flattening within individuals suggests that all parts of the exoskeleton responded similarly to dissolution.

Plastically deformed specimens show no evidence of wrinkled cuticles, such as are common, for example, in the associated phosphatic aglaspidids (Briggs and Fortey, 1982; Hesselbo, 1987a). Wrinkling has also been recorded in trilobites from elsewhere such as poorly calcified olenellids (Harrington, 1959), *Paradoxides* (Bergström and Levi-Setti, 1978), and trilobites interpreted to represent post-molt individuals where full calcification had not been completed (Whittington, 1980; Miller and Clarkson, 1980; Speyer, 1985). Plastic deformation without wrinkling probably implies that the exoskeleton of *Dikelocephalus* had disolved completely proir to compaction. Early dissolution of the cuticle suggests that cuticular calcite was unstable compared to that of the matrix and that in some cases the formation of composite molds began soon after burial (McAlester, 1962; Bambach, 1973). Compaction sometimes serves to enhance subtle features of glabellar structure, such as the intercalated furrows (Pl. 5, Figs. 6,7).

Interbedded sands and clays responded differently to compression. Continued dewatering of the clays subsequent to sand cementation resulted in irregular warping of large sclerites (Pl. 2, Figs. 5,6) and to the buckling of partially cemented sand layers. Early cementation of the sand laminae suggests that waters saturated in carbonate ions (all cements in the Croixan Series are carbonate cements) passed through these interbeds as the clay layers continued to dewater. Cuticle dissolution in the clay layers might have been a source of this carbonate.

Effects of deformation on the taxonomy of dikelocephalids

Whilst *Dikelocephalus* specimens from the northern Mississippi Valley are free from tectonic distortion and most have suffered relatively little compression, deformation has contributed to previous taxonomic errors. Compaction-related deformation can have a marked effect on the appearance of trilobite sclerites (Fortey, 1974), through distortion of both the original shape and of key taxonomic features (Hughes and Rushton, 1990; Hughes and Jell, 1992). The effects of deformation must be considered when character variation is assessed.

Hall (1863) suggested that the sagittal portion of the frontal area is extended into a short spine in some specimens of *Dikelocephalus*. He considered this characteristic of a new ''variety'' of *Dikelocephalus minnesotensis*. The anterior extension is clearly a taphonomic artifact due to fracture of the frontal area (Pl. 3, Figs. 1,2). Although Whitfield (1882) noted the effects of compression on the relief of sclerites, Ulrich and Resser (1930 p. 18) considered ''contour'' as a important character for use in the discrimination of species of *Dikelocephalus*. For example, in the description of *D. subplanus* (*op. cit.* p. 45), they suggested that the ''flatness of the middle and marginal parts of the free cheeks'' are important characters linking *D. subplanus* with *D. gracilis*, and serve to distinguish these species from *D. minnesotensis* (*sensu* Ulrich and Resser, 1930). A disarticulated cephalon was used as a syntype of *D. subplanus* (Ulrch and Resser, 1930, pl. 14, fig. 4). The glabella is fractured and the intraocular fixed cheek has been flattened and depressed on the left hand side. This suggests that the associated free cheeks may also be flattened due to compaction. Hence 'contour' is a dubious character for use in the designation of this species. Westrop (1986a) considered the effect of compaction on the cranidial morphology of the related trilobite *Walcottaspis* and suggested that the different appearance of the glabella in *Walcottaspis* and *Dikelocephalus* was due to compaction.

Labandeira (1983a, figs. 9, 10) compared the positions of the left and right palpebral lobes in about a hundred of Ulrich and Resser's specimens of *Dikelocephalus* to test whether bilaterally symmetrical characters differed between sides. No statistically significant differences between left and right palpebral lobes were detected, and Labandeira (1983a, p. 130) concluded that distortion had little effect on character morphology. Labandeira's (1983a) analysis included measurements from specimens preserved in sandstones. These specimens showed no significant differences from those preserved in fine-grained interbeds in the heterolithic facies, and showed a similar range of morphological variability. Thus comparable measurements could be taken from specimens preserved in either lithology.

These observations indicate that, provided sclerites are first carefully scrutinised to eliminate those which are distorted, it is possible to perform morphometric analysis of *Dikelocephalus* to assess biological variation. However some characters are more liable to distortion, or less frequently preserved, and must be reflected in the choice of characters used in morphometric analysis.

Fragmentation

Trilobite exoskeletons are made up of many individual sclerites that may disarticulate after molting or death. Fragmentation refers to the breakage of individual sclerites. Such fragmentation has been interpreted as indicative of sclerite transportation (Brett and Baird, 1986; Speyer and Brett, 1986). Susceptibility to fragmentation increases as decay weakens the cuticle (Allison, 1986).

It is frequently difficult to assess the degree of fragmentation of *Dikelocephalus* sclerites because they are so large. Slabs are often too small to accommodate the entire sclerite. When the rock fractures much of the sclerite is left unexposed as the plane of rock fracture may not coincide with the entire surface of the sclerite. Excavation of larger sclerites almost invariably reveals an extension hidden in the matrix, suggesting that they are not fragmented (*contra* C.W. Byers, 1978; R.A. Byers, 1979). Smaller sclerites frequently preserve very delicate features, such as genal and postlateral spines, still intact. In these specimens there is no evidence of fragmentation. Many yoked free cheeks (joined by a thin strip of ventral doublure) of *Dikelocephalus* are found as isolated sclerites (*e.g.* Ulrch and Resser, 1930, pl. 14, fig. 4) indicating that transportation cannot have been long distance (Fortey, 1975).

The degree of fragmentation of *Dikelocephalus* and other trilobites from the St Lawrence Formation appears to be rather low. This does not imply that the sclerites were totally unaffected by transportation (Allison, 1986). Rather, the lack of evidence of abrasion or fragmentation suggests that transportation after exoskeletal disarticulation was slight.

Disarticulation of sclerites

Disarticulation can result from decay of exuvae, scavenging, bioturbation or current transportation (Henningsmoen, 1975; Mikulic, 1990). The degree of disarticulation can show marked spatial variation in response to different environmental conditions (Speyer and Brett, 1986).

Articulated specimens of *Dikelocephalus* are extremely rare (<1% of samples). The overwhelming majority of specimens are preserved as 'isolated' sclerites (*sensu* Henningsmoen, 1975). Thus post-mortem processes were effective in disturbing sclerite orientation after death (Speyer and Brett, 1986). Because of the molting habit, the majority of sclerites represent exuviae rather than dead individuals (Henningsmoen, 1975; Sheldon, 1988). Several specimens show associations of sclerties that are very likely parts of the same individual. These associations could not have been transported because many of the sclerites are detached (Pl. 4, Figs. 1,2; Henningsmoen, 1975; Fortey, 1975). The regular configuration of sclerites in some associations (Pl. 3, Figs. 3,4) may suggest either molting behaviour (and subsequent collaspse of exuvae), or specific predator/scavanger activity. Associations of detached sclerites from the same individual indicate that at times sedimentation rates were high enough to bury and preserve associations.

Dikelocephalus sclerite distribution within sediments

Dikelocephalus is most commonly found in fine-grained units of the heterolithic St Lawrence Formation (Hesselbo, 1987b). Horizons in which sclerites are concentrated are lithologically identical to unfossiliferous units. The thickness of fossiliferous horizons varies, but is usually between 3-30 cm. They may represent periods of slow sedimentation (see Kidwell, 1986). Fossiliferous horizons are polytypic (*sensu* Kidwell, Fürsich and Aigner, 1986), containing a variety of invertebrate macrofossils including other trilobites, aglaspidids, dendroids, hyolithids, conularids, serpulids, echinoderms, gastropods and inarticulate brachiopods (Ulrich and Resser, 1930; Ruedemann, 1933; Raasch, 1939; Hesselbo, 1987a).

Most sclerites lie parallel to bedding (concordant orientation), and are almost always matrix-supported. Occasionally sclerites overlap, forming a bioclast-supported skeletal pavement (Kidwell, Fürsich and Aigner, 1986; Pl. 4, Fig. 3). In plan view sclerites show no obvious orientation. Several specimens from North Freedom Bed 8 were found orientated oblique to bedding, possibly as a result of bioturbation. There are no vertical trends in taxonomic composition or sclerite size within any individual bed.

Taphonomic studies of disarticulated sclerites

A study of three fossiliferous horizons from the heterolithic facies allows some generalizations to be made about the nature of accumulations of disarticulated sclerites.

1. Size sorting

The size distributions of disarticulated cranidia and pygidia from North Freedom Beds 2 and 8 and Arcadia Bed 18 were analysed (Figs. 3,4). The excess of small cranidia over small pygidia is due to the method of measuring. Cranidium size values represent the occipital glabellar length (b_1), not the entire length of the cranidium. Pygidium values represent the intra-articulating pygidial length (z_1; Shaw, 1957), which is almost the entire length of the pygidium. If the entire length of the cranidium was plotted the size ranges of cranidia and pygidia would be identical. Complete specimens show that adult *Dikelocephalus* was isopygous—the cranidium and pygidium were of similar lengths (Hughes, 1990,1991a). The size ranges and mean size values of cranidia and pygidia are very similar within each bed (Figs. 3,4), resembling the original ratios in living *Dikelocephalus*. This is what would be expected if the disarticulated sclerites suffered little post molt/post mortem sorting.

All six localities investigated from the St Lawrence Formation show a wide range of sclerite sizes, indicating that size-sorting was mimimal (Figs. 3,4). Although there are some differences in the shape of each of the graphs (*e.g.* the cranidial and pygidial distributions from Arcadia are slightly left-skewed, whereas those from North Freedom approach a normal distribution), most distributions are unimodal. Bimodal distributions of pygidia occur in Beds 2 and 8 from North Freedom, but the significance of this bimodality is questionable, given the relatively small sample sizes (see Sheldon, 1988). Normal distributions can indicate size sorting (see Raup and Stanley, 1985), but may also develop depending on growth rates and survivorship within fossil populations (Craig and Hallam, 1963; Sheldon, 1988). With the possible exception of the pygidium size distribution from Arcadia Bed 18 (Fig. 4c), each distribution is rather broad and flat, resembling those recorded in a variety of Middle Ordovician trilobites from basinal mudstones, which are known to be untransported (Sheldon, 1988). Hence the size distributions of *Dikelocephalus* indicate a low degree of size sorting. This situation contrasts with that recorded in Upper Cambrian tempestites from southern Alberta, where small holaspids have been transported offshore by storm activity (Westrop, 1986b).

The smallest growth stages of *Dikelocephalus* (and other trilobites) are consistently absent from northern Mississippi Valley deposits (Figs. 3, 4). This is unlikely to be due to the selective winnowing of small sclerites, because many very small fragments of brachiopods and aglaspidids are present in the same beds as large *Dikelocephalus*. Sheldon (1988) suggested that normal distributions result from steady-state populations of post-larval trilobites. Pre-adult trilobites were frequently recorded in his examples, however, and formed 3.9% of the population of the trilobite *Ogygiocarella*, which has a size range comparable to that of *Dikelocephalus*. Additional factors may be responsible for the absence of smaller growth stages of *Dikelocephalus*. These include the relatively labile nature of the cuticle of immature instars (Sheldon, 1988; Speyer and Chatterton, 1989), and the possibility that immature forms did not inhabit the region.

Another way of assessing the effect of size sorting is to compare the relative abundance of genera of different sizes. Relative abundances from fine-grained heterolithic beds were investigated from three widely spaced sections within the northern Mississippi Valley (see Figs. 2,5). All localities show a similar range of large and small taxa (Fig. 5). Thus, size distributions of a range of St Lawrence Formation trilobites indicate that size sorting has been minimal.

2. Shape-sorting

Experiments by Hesselbo (1987a,b) showed that model cranidia settle upside-down through still water, whilst pygidia settled in the normal, dorsal uppermost, orientation. He noted that the same configuration was common in *Dikelocephalus* sclerites from North Freedom Bed 2, and suggested that the orientation of disarticulated sclerites was the result of sedimentologically controlled resuspension followed by settling. However, cranidia may have been detached and inverted during molting, collapse of exuviated exoskeletons (see below) or due to predator/scavanger activity, possibilities which Hesselbo (1987a,b) did not consider.

Complete specimens suggest that adult *Dikelocephalus* had a minimum of nine thoracic segments (Hughes, 1990). Hence a totally undisturbed assemblage should include at least nine segments for every pair of free cheeks, and every cranidium, hypostome and pygidium (Fig. 6a). The relative abundance of sclerites was assessed in four localities from the heterolithic facies (Fig. 6b-e). All localities have fewer than the predicted number of thoracic segments and hypostomes, whereas cranidia and pygidia are over-represented. Localities differ in the relative abundance of thoracic segments, and in the ratio of cranidia to pygidia. At Lucas the proportion of thoracic segments is 7:5, which approaches the predicted 9:5 ratio (9 being the minimum number of thoracic segments in adult *Dikelocephalus*, 5 the total number of other sclerites). The ratios for all other localities falls well below expected values. That at Arcadia, for example, is 4:9. At North Freedom the numbers of cranidia and pygidia are very similar, but at both Arcadia and at Lucas the number of pygidia greatly exceeds that of cranidia.

Under-representation of thoracic segments and hypostomes has been recorded in other studies of disarticulated trilobites (Speyer and Brett, 1986; Mikulic, 1990). Collecting bias might enhance the disparity between predicted and observed segment/cranidia ratios. Fine-grained units of the heterolithic facies split more readily along broad, flat surfaces, such as cranidia or pygidia, than along narrow thoracic segments. A similar argument was advanced by Sellwood (1966) to explain why more pygidia than cranidia are found of some thysanopeltids from the Devonian of southern Britain. However, the ratio of thoracic segments to cranidia in *Dikelocephalus* is locally variable suggesting that collecting bias alone does not explain this feature. Selective winnowing of thoracic segments (and, possibly, of hypostomes) might reduce their abundance (Hesselbo, 1987a,b). If so, some localities should contain concentrations of these sclerites. However, the ratio of thoracic segments (or hypostomes) nowhere exceeds the predicted number of cranidia/pygidia. Neither is there evidence that thoracic segments and hypostomes were more subject to fracturing than cranidia or pygidia, which could explain the disparity without invoking selective transport.

The hydrodynamics of trilobite sclerites are poorly known (Hesselbo, 1987a,b; Mikulic, 1990). However, as there is little evidence that fragmentation or disintegration selectively affected one sclerite type more than any other, it seems likely that sorting based on sclerite shape has been at least partially responsible for departure from predicted sclerite abundance ratios.

Implications of taphonomy for *Dikelocephalus* distribution studies

Shape sorting studies suggest that some lateral transportation of sclerites may have occurred, but the lithology of the deposits, coupled with the size distribution and good preservation of the sclerites suggest that any transportation has been short distance. This interpretation agrees with evidence on the sedimentary environment (Hughes, 1990) and with other paleontological studies which suggest that, in similar sedimentary environments, macrofossils are largely untransported (Kreisa and Bambach, 1982; Aigner, 1982). Modern shallow marine environments also show very little post-mortem sorting of marcofaunal assemblages (MacDonald, 1976; Warme *et al.* 1976) and fine spatial variations in living assemblages are mirrored in ''dead assemblages'' (Valentine, 1989). Thus the distribution of sclerites can be assumed to represent the original distribution of *Dikelocephalus* at the time of molting or death and thus provide a suitable basis for a study of biologically-controlled variation.

FUNCTIONAL MORPHOLOGY

General body plan

From three nearly complete specimens (Hughes, 1990, 1991a) the length to width ratio of the dorsal shield is estimated to be about 1.3, indicating that the trilobite has a roughly circular shape. It has a broad pleural region, eyes within the dorsal surface, a narrow rachis, and a very broad doublure. Material preserved with original relief (Pl. 1, Figs. 1-4; Pl. 2, Figs. 3,4) suggests that the dorsal shield of *Dikelocephalus* was rather flat and that the shape resembles an inverted saucer. *Dikelocephalus* grew to gigantic sizes. Even the smallest sclerites appear to be holaspid, and suggest individuals about 1.5 cm long (based on estimates derived from complete specimens). The largest sclerites (Pl. 2, Figs. 5,7; Pl. 4, Figs. 4,5) suggest individuals 40 to 45 cm long. As *Dikelocephalus* was exceptionally broad, the total area of the dorsal shield of a large individual is one of the largest of any known trilobite.

Dikelocephalus is similar to most other trilobites in that the exoskeleton is dorsoventrally flattened with the eyes on the dorsal surface. These features suggest a benthic or nektobenthic life mode (Fortey, 1985). The unusually large size attained by some individuals, in addition to the rounded shape, the isopygous condition and the wide extent of the doublure, sets *Dikelocephalus* apart from the generalised ptychoparioid morphotype (*sensu* Jell, 1981). Excluding certain other members of the Dikelocephalacea, the gross morphology of *Dikelocephalus* is most similar to some advanced members of the Asaphida (*sensu* Fortey, 1990), particularly asaphids such as *Ogygiocarella* and nileids such as *Homalopteon* (see Fortey, 1986). This does not necessarily imply a close phylogenetic relationship but may indicate comparable life strategies. Experiments with casts of *Ogygiocarella* bucked and planed in gentle currents when suspended within a flume showing that this morphology is poorly suited to free movement within the water column (Fortey, 1985). However, when settled on the floor of the flume, the casts resisted movement even in strong currents, and Fortey suggested that this may reflect the life preference of *Ogygiocarella*. A bottom-hugging life mode is also consistent with the gross morphology of *Dikelocephalus*.

Functional aspects the cephalon

Cephalic border

Those *Dikelocephalus* which possess a prominent cranidial border often preserve pits in the anterior border furrow and caeca. The same relationship occurs in *Balnibarbi* and some other olenids (Fortey, 1974). Fortey (1974) suggested that the tubular rim of the cephalic border of trilobites may have enclosed circum-cephalic organs and that the pits could have had a sensory or strengthening function. The irregular development of the pits within individual specimens makes it unlikely that they form part of an integrated sensory system. The correspondence between pits on the dorsal surface and nodes on the doublure recorded in *Balnibarbi* (Fortey, 1974) is not present in *Dikelocephalus*.

Trilobite caeca are variable in form and may represent several different types of internal organ (Fortey, 1974; Jell, 1978). Those in *Dikelocephalus* (Pl. 4, Figs. 6-8) are many times larger than the branched (''type 4'') caeca recognised in ptychoparioids (Jell, 1978), even when relative size differences are taken into account. This large size suggests that a respiratory function for the caeca is unlikely in *Dikelocephalus*. Type 4 caeca are most common in trilobites that inhabited oxygen-poor environments (Jell, 1978). Sedimentological and trace fossil evidence suggests that the local seafloor during the Sunwaptan was well-oxygenated. Thus the caeca in *Dikelocephalus* were probably unrelated to respiration, but their function is unknown.

Frontal area

Marked variability of the frontal area of *Dikelocephalus* (Hughes, 1990, 1991a) partly reflects the degree of retraction of the dorsal facial suture from the anterior cephalic margin. The functional significance of retraction is unknown. There is no obvious relationship between the sedimentary environment and frontal area morphology. The transverse distance between the anterior of the palpebral lobe and the margin of the glabella does not appear to be related to the angle of divergence of the facial suture, as has been observed in some olenid trilobites (Fortey, 1974).

Eye orientation and size

The eye of *Dikelocephalus* is perched high on the ocular platform, with an unobstructed field of vision, as is common in benthic trilobites (Fortey, 1985). The visual surface of *Dikelocephalus* is not preserved and was probably separated from the rest of the cephalon by the circumocular suture. Specimens preserved in three dimensions suggest that the visual surface was positioned vertically between the palpebral lobe and the marginal flange on the free cheek (Pl. 5, Figs. 1-3). If the visual surface was flat (*i.e.* not curved) in a vertical section, then the field of view in the vertical plane was restricted to a thin band. If the upper and lower margins of the eye were horizontal, as has been suggested for many trilobites (*e.g.* Clarkson, 1966a,b; Bergström, 1973; Thomas and Lane, 1984), the genal spines would slope downwards posteriorly (Pl. 5, Figs. 4,5). In this condition the long genal spines of *Dikelocephalus* would dip well below the tips of the thoracic pleurae. This orientation therefore seems unlikely, given the dorso-ventrally flattened form of *Dikelocephalus*. It is more likely that the visual surfaces sloped gently anteriorly, and that the margin of the free cheek was roughly parallel to the dorso-ventral plane of the thorax.

Assuming that the length of the visual surface corresponds to the length of the palpebral lobe, the longitudinal field of vision (*sensu* Clarkson, 1966a) of the each eye probably extended through about 180°. In larger specimens the longitudinal field of vision was slightly restricted posteriorly, due to negative allometry of the eye (Hughes, 1990, 1991a). Thus *Dikelocephalus* had good all around lateral vision, although it probably could not see directly in front of the glabella. The slope of the eye suggests that *Dikelocephalus* may have looked downwards anteriorly. As nothing is known of the eye structure (although it was almost certainly holochroal), caution is required when suggesting possible functional explanations for the decrease in the relative size of the eye during growth. The internal structure of holochroal eyes can vary markedly within individuals and there is no clear relationship between eye size and visual acuity (Clarkson, 1979). However, it may be that the eye functions best at or above a certain size, and that growth of the eye has to be relatively fast during early ontogeny to achieve this optimum. Once this size is reached, eye growth continues at a steady rate. Locality-based differences in palpebral lobe growth do occur, and may suggest a pattern of inter-populational heterochrony (Hughes, 1990, 1991a). The large eyes in the Arcadia population could reflect a functional response, but there is no independent evidence to suggest environmental conditions which favored large eyes.

Glabella

Dikelocephalus possesses a broad glabella which is quite convex when compared to that of other large trilobites, such as *Ogygiocarella*. Glabellar furrows are thought to reflect muscle attachment areas (Bergström, 1973; Fortey, 1974). The firm incision and wide extent of the occipital and first two pairs of glabellar furrows suggest that substantial muscles were attached to them. They shallow abruptly medially (Pl. 5, Figs. 6,7), probably reflecting the position of the gut, running along the sagittal axis close beneath the dorsal exoskeleton (Cisne, 1975). The furrows tend to be more marked toward the rear of the glabella, which may reflect larger posterior muscle pairs. As these muscles are thought to have been attached to the limbs, this trend might reflect successively weaker limbs toward the anterior of the cephalon (Bergström, 1973). The absence of the third pair of glabellar furrows in large cranidia does not imply that the anterior limbs were absent (many effaced species lack glabellar furrows), and there may have been four pairs of cephalic appendages in *Dikelocephalus*, as in some other trilobites (Bergström, 1973). The function of the intercalated furrows on L0-L3 is unknown. They may represent the apodomes of additional muscles housed under the glabella. Muscle scars intercalated between glabellar furrows have been documented in phacopids (Eldredge, 1971).

The function of the median glabellar tubercle varied among different trilobites (Fortey and Clarkson, 1976). The internal structure of the tubercle in *Dikelocephalus* could not be determined due to preservation as composite molds. However, the position of the glabellar median tubercle with respect to the eyes, its upstanding nature and its homology with thoracic median tubercles discount a visual function in *Dikelocephalus*. In some modern decapods the dorsal median tubercle may have a sensory function during early ontogeny (Barrientos and Laverack, 1986). Sexual differences are a possible explanation for the tubercle dimorphism in *Dikelocephalus*. In *Phacops schotheimi schotheimi* a form with small median tubercles and another with large median tubercles have been interpreted as sexual dimorphs (Sellwood and Burton, 1969). However, the occurrence of the thoracic median tubercle in *Dikelocephalus* is much less common than the occipital median tubercle. This suggests considerable intra-populational variation in the development of median tubercles on the rachis. Other members of the Dikelocephalacea possess a median occipital spine (Ulrich and Resser, 1933). *Prosaukia* and *Calvinella* show greatly variable degrees of spine development. Rachial spine and tubercle development appears to be highly plastic among dikelocephalids.

Median suture

The median suture may have assisted molting in some trilobites (Henningsmoen, 1975), but it is not known if a functional median suture was essential during exuviation of *Dikelocephalus*. Possible molt ensembles show yoked free cheeks (Pl. 3, Figs. 3,4).

Hypostome

The hypostome was docked against the ventral doublure (Pl. 5, Fig. 8) in the conterminant position (Fortey and Chatterton, 1988). With the material available at present it is not possible to assess whether the anterior wings of the hypostome were braced against the ridge formed by the axial furrow on the internal surface of the cephalon (Whittington, 1988a). It is probable that they did, because the wings are well-developed and lay directly below the anterolateral margins of the glabella. Flexible articulation of the hypostome during life is unlikely.

Material preserved with original relief shows that the doublure lay close beneath the dorsal surface (Pl. 5, Figs. 4,5). As the hypostome was attached to the inner margin of the doublure it lay close beneath the glabella (Pl. 5, Fig. 8). The pleural parts of the cephalon formed a broad, downsloping marginal flange, and hence the hypostome lay at a level above the lateral cephalic margin. Fortey (1986) observed a similar condition in the asaphid *Symphysurus palpebrosus* and deduced that direct ingestion of sediment would not have been possible.

The maculae of many trilobites are smooth (Whittington, 1988b) and a macula may have been present in larger specimens of *Dikelocephalus* but was obscured due to progressive effacement during ontogeny (Hughes, 1990; 1991a). The function of the maculae is poorly known. Suggestions include ventral eyes, areas of muscle attachment (see Whittington, 1988b) or statocysts (Hu, 1971). The maculae of *Dikelocephalus* are too poorly preserved to permit further functional analysis.

Functional aspects the thorax

The rarity of articulated exoskeletons from Cambrian shelf environments in north America has constrained the study of the functional morphology of trilobites from these environments (Stitt, 1976). No articulated thoraxes of *Dikelocephalus* have been described. The complete specimen illustrated by Labandeira (1983a) as *Dikelocephalus minnesotensis* belongs to the saukiid genus *Tellerina*. Three reasonably complete dorsal shields of *Dikelocephalus* are now known (Hughes, 1990, 1991a) and other specimens preserve more than three articulated sclerites (Pl. 5, Figs. 9,10). Other specimens show the close association of several sclerites and probably represent individuals (*e.g.* Pl. 3, Figs. 3,4; Pl. 4, Figs. 1,2). Incomplete preservation constrains functional interpretations of thoracic articulation.

The possession of a well-developed articulating half ring and a broad anterior facet on each thoracic segment and on the pygidium (e.g. Pl. 6, Figs. 1,2), suggests that these sclerites could articulate. The anterior edge of each pleural region was straight for only a short distance from the axial furrow, indicating that the hinge was short and the fulcrum quite close to the axial furrow. During flexure, transverse terrace ridges on the anterior facet of the propleurae, termed the ''petaloid facet'' by Fortey (1986), intersected longitudinal terraces on the doublure of the preceding segment (Pl. 2, Fig. 7). The petaloid facet in *Dikelocephalus* apparently lacked the transverse ridge which is developed at the top of the facet in *Symphysurus* (see Fortey, 1986). The opisthopleural node (Pl. 4, Fig. 5) could have limited the degree of enrolment, by acting as an obstacle to movement beneath the posterior margin of the preceding segment. However, as the node is positioned far back on the pleural region, it is unlikely that it would have come into contact with the preceding segment during flexure. The node may have a different and unknown function.

Variations in the shape of thoracic segments can be used to infer the pattern of thoracic flexure (Stitt, 1976; Fortey, 1979). The articulating half ring on the first thoracic segment appears to be quite long, if its extent is reflected in the position of the ring furrow (*sensu* Henningsmoen, 1960) on the occipital lobe. Thus there may have been considerable flexure at the junction between the cephalon and the thorax. The general trend of increasing half ring length along the thorax suggests that posterior segments could flex more than anterior ones (Pl. 6, Figs. 1,2). The posterior increase in the transverse extent of the articulating facet supports this suggestion. The pygidium does not have an unusually long articulating half ring. Articulation between the thorax and pygidium was probably limited.

The arrangement of sclerites in possible molt ensembles (Pl. 3, Figs. 3,4), and the preservation of partially enrolled sets of segments (Pl. 5, Figs. 9,10), suggest that ventral flexure was a natural life attitude in *Dikelocephalus*. The extent to which *Dikelocephalus* enrolled is not known. Considerable flexure would have been possible in the thorax, but there is no evidence of any coaptative structures. The relative proportions of cranidium, thorax and pygidium, and the morphology of the pleural spines, suggest that if enrolment occurred it must have been cylindrical (*sensu* Bergström, 1973), in which case internal soft parts would not have been completely enclosed by the dorsal shield. As the environment is unsuitable for the preservation of enrolled trilobites (Speyer, 1985) the absence of enrolled specimens is not surprising.

Fortey (1986) suggested that the petaloid facet permitted exchange of oxygenated waters during complete enrolment. As enrolment in *Dikelocephalus* was cylindrical, the internal organs would have maintained direct contact with the external environment. It seems unlikely that water flow across the petaloid facet was necessary to support respiration in this case and Fortey's (1986) interpretation may not apply to *Dikelocephalus*. A possible alternative function for the petaloid facet could be to reduce friction between the articulating facet and the doublure of the preceding segment by restricting the area of contact between the two surfaces during flexure to the narrow crests of the ridges. The presence of the petaloid facet is considered synapomorphic for a clade of advanced asaphid trilobites including the Ceratopygidae, Asaphidae, Taihungshaniidae, Nileidae and Cyclopygidae (Fortey and Chatterton, 1988). Its discovery in *Dikelocephalus* means that further investigation of this character is required.

Functional aspects the pygidium

Little is known of the functional controls of pygidial morphology. The four well-defined axial rings imply the presence of at least four pairs of pygidial appendages. The two additional incomplete furrows may correspond to further appendages. The post-axial ridges and post-axial emargination may have accommodated the terminal portion of the gut and the anus. The functional significance of the variation in division of the pleurae is unknown. The posterolateral spines may have functioned to maintain stability during movement or to provide support whilst at rest on the seafloor, but there is no positive evidence for their role. The petaloid facet on the articulating facet of the pygidium is similar to those of the thoracic segments and presumably functioned in the same way.

Functional aspects cuticular ornament

Pustules

The dorsal ornament of *Dikelocephalus* varies markedly in different parts of the exoskeleton. Pustules are generally restricted to the rachis, but in a few specimens they are found on the adaxial parts of the pleural region of the pygidium (Pl. 6, Figs. 3,4). Pustules are confined to higher regions of the exoskeleton, and are absent on the lateral margins, and within furrows on the dorsal surface. At the anterior of the glabella pustules become elongated and grade into inosculate terrace ridges (Pl. 1, Fig. 7). A similar transition is observed in many trilobites (Eldredge, 1972; Fortey, 1974; Campbell, 1977; Ludvigsen, 1979; and Hammann, 1985). However, terraces do not show progressive ontogenetic effacement and do not migrate into pustulated areas. Pustules are not replaced by terraces during ontogeny. Hence the developmental controls of pustulation and terracing appear to be independent. The progressive decline in the numbers of pustules, decrease in density of pustulation, and restriction of pustules towards the axis, suggest that the function performed by them was of less importance to large individuals than to smaller ones. However, the absence of prominent pustules in large specimens does not necessarily imply that the function they performed had become totally obsolete. If the pustules housed sensory organs, for example, it is possible that such organs lacked a marked expression on the surface of the cuticle in larger individuals.

Interpretation of the function of pustules in *Dikelocephalus* is very difficult because their internal structure cannot be determined (see above). A wide range of sensory functions, including acting as photo- and chemo-receptors, have been proposed (Miller 1976; Størmer, 1980; Hammann, 1985). Coarse tubercles have also been interpreted has having a strengthening function. In *Neseuretus* the larger pustules or ''macrotubercles'' are thought to have housed hairs responsible for the removal of sediment from the dorsal exoskeleton (Hammann, 1985). The pustules in *Dikelocephalus* are of similar size to these macrotubercles. If the pustules were involved in removing sediment it is not clear why they are restricted to the sagittal axis.

Dorsal terrace ridges

Petaloid facets form only a small proportion of the total area of the dorsal shield over which terrace ridges are developed. Terraces cover most of the pleural region but are absent in furrows. Dorsal terraces are strikingly different from ventral terraces (they do not represent the composite impressions of ventral terraces on the dorsal surface: Pl. 1, Figs. 2-4).

In *Dikelocephalus* straight-crested terrace ridges run along the anterolateral border of the cephalon (Pl. 2, Fig. 2). Terraces become inosculate or granulate over the higher parts of the exoskeleton (Pl. 1, Fig. 3; Pl. 6, Fig 5) or are replaced by polygonal patterns (Pl. 1, Fig. 2). At the top of the ocular platform the terraces have steep dips on both sides; they are elongate ridges rather than cuesta-form (Pl. 6, Fig. 5). On the pleural platform of the pygidium terraces are crescentic (Pl. 1, Fig. 3). Terraces on the dorsal surface face peripherally (Miller, 1975; *contra* Schmalfuss, 1978b, 1981). This orientation would oppose movement of sediment over the dorsal shield during burial (Fortey, 1979) and hence the dorsal ornament was not adapted to facilitate burrowing. The marginal terraces may have helped to keep the dorsal surface free by facilitating sediment movement toward the margin. However, the inosculate, symmetrical ridges on the ocular platform are not obviously adapted to perform this function. The terracing patterns in *Dikelocephalus* are not consistent with a burrowing life mode.

Ventral terrace ridges

Ventral terraces on the doublure are much more regular than those on the dorsal surface. They face peripherally, are straight-crested or slightly wavy, and cuesta-form. They are concentrated at both peripheral margins of the doublure (Pl. 6, Fig. 5) and show an isometric growth relationship (Hughes, 1990). As the doublure lies close beneath the dorsal surface and extends almost as far as the rachis (Pl. 6, Figs. 6,7) most ventral terraces could not have been in contact with the sediment during life (also see Fortey, 1985). The isometric growth relationship contrasts with the pattern of ''allometric densing'' in terrace ridge spacing (Schmalfuss, 1978a,b; 1981) thought to be characteristic of forms in which the terraces lay in contact with loose sediment (but see Savazzi, 1985). The similarity of terrace spacing in *Dikelocephalus* living in fine sands and mudstones also suggests that there is no close relationship between terrace spacing and grain-size.

The complex terracing pattern on the hypostome (Pl. 7, Figs 1,2) contrasts with the pattern developed on the doublure. Terraces on the lateral borders are straight-crested and asymmetric (Pl. 7, Fig. 3). Ridges are deflected about the maculae and they become concentric about the mid-point of the median body. On the median body the terraces are steep on both sides (Pl. 7, Fig. 4), resembling those developed on the ocular platform.

Although there has been much recent interest in cuticular terraces in a wide range of invertebrates their function is not well known, even in extant forms (Savazzi, 1985 and references therein). It is clear that terrace ridges performed different functions on different parts of the trilobite exoskeleton (Fortey, 1986) and that no single functional explanation will account for all patterns of terracing.

Molting

The taphonomic regime of the St Lawrence Formation does not favor the intact preservation of molt ensembles (see above). Few articulated sclerites of any trilobite are known from the northern Mississippi Valley. Hence the absence of repeated configurations of *Dikelocephalus* sclerites is not surprising, but makes interpretation of molting behaviour very difficult. Some sclerites show arrangements that suggest that taphonomic disturbance was slight. Two of the three ''complete'' dorsal shields show telescoping of some sclerites, or loss of the cranidium (Hughes, 1990). In both these specimens the rachis appears to be slightly flexed and it is possible that they represent molts (see Henningsmoen, 1975). However, there is no positive evidence that these are molt ensembles rather than carcasses. Individual trilobites may have molted in a variety of ways (Speyer, 1985) and most ensembles are not thought to represent ''normal'' molting behaviour (McNamara and Rudkin, 1984; McNamara, 1986). As the preservation of sclerites in exuvation orientation requires exceptional conditions of preservation, caution is required when interpreting sclerite associations as molt ensembles (Whittington, 1990).

Abnormalities

Although there is considerable morphological variation within *Dikelocephalus*, and limited bilateral asymmetry, morphological features of some specimens stand out as being particularly unusual. A cranidium from North Freedom Bed 2 shows a large bulbous swelling on the anterior lobe of the glabella (Pl. 7, Figs. 5,6). The swelling has a central depression, which may have resulted from compaction. Similar structures have been recorded on the glabellae of several other trilobites and are thought to be due to parasitism (Owen, 1985; Jell, 1990).

Abnormalities are most often recorded on the pygidium of *Dikelocephalus*, as in other trilobites (Owen, 1985). A spectacular example in which the rachis and pleurae are both affected (Pl. 7, Fig. 7) shows incomplete development of the fourth rachial ring and an unusual pattern of bifurcation of the pleural ribs. Similar patterns of convergence and bifurcation of the ribs are evident in several other specimens (*e.g.* Pl. 3, Fig. 5). Owen's (1852) syntype pygidium of *Dikelocephalus* shows an abnormality of this type. The lateral margins of several pygidia show arcuate embayments (Pl. 7. Fig. 8) with callused margins in some cases (Pl. 3, Fig. 6). The causes of trilobite abnormalities are poorly known (Owen, 1985). The arcuate embayments may represent the activity of predators (Conway Morris and Jenkins, 1985). Considering the large sample size (over 2750 specimens examined) these abnormalities are rather uncommon in *Dikelocephalus* compared to some other Cambrian trilobites (L.E. Babcock, pers. comm).

Many specimens show irregular, sinuous trails developed between the dorsal surface and the doublure. These are present in cephala (Pl. 4, Fig. 4), thoracic segments, and are common in pygidia (Pl. 3, Fig. 6; Pl. 7, Fig. 8). They form upstanding ridges on the internal molds and probably represent borings into the internal surface of the exoskeleton. They generally run abaxially from near the internal margin of the doublure, although they are frequently irregular. A similar radiating pattern of borings was described in *Aphelaspis tarda* by Hu (1983), who suggested that they were caused by nematodes. The borings in *Dikelocephalus* are considerably larger than those attributed to fungal infection in *Asaphus raniceps* by Dalingwater (1975).

Autecology

As no pre-holaspid specimens have been observed, little is known about the early ontogeny of *Dikelocephalus*. The lack of immature specimens is partly be due to taphonomic factors (see above) but may also reflect the fact that *Dikelocephalus* could have had a pelagic, asaphoid-type protaspis (Fortey and Chatterton, 1988; Speyer and Chatterton, 1989).

The aspect of the eyes, and the flat morphology of the dorsal shield suggest that holaspid *Dikelocephalus* was benthic. The flattened morphology and relatively narrow rachis suggest that the area for muscle attachment was smaller than in many other trilobites, hence *Dikelocephalus* may have moved slowly compared to some more convex forms (see Fortey, 1985). The size of the eyes suggests that vision was important for *Dikelocephalus* and make a permanently infaunal life mode unlikely. The disc-like shape would have impeded burrowing. There is no positive evidence for an infaunal life mode. The architecture of the exoskeleton suggests that *Dikelocephalus* was able to flex the thorax, although how far it could enrol is unknown. If enrolment did occur the softparts were not completely enclosed by the exoskeleton. Some sclerite associations suggest flexure of the thorax during molting. The feeding mode of *Dikelocephalus* is unknown. Direct consumption of sediment is unlikely. Filter feeding or predation/scavenging are possible modes of life, but there is no strong evidence in favor of either.

Suggestions about life mode based solely on morphological criteria can be tested against independent sources of evidence (Fortey, 1985). Sedimentological studies suggest that the St. Lawrence Formation was deposited in shallow marine conditions of normal salinity, subject to occasional storms and periodic exposure. The flattened, rounded shape of *Dikelocephalus* is consistent with life in this environment because such a morphology would resist movement even in strong currents if the trilobite were settled on the substrate (Fortey, 1985). The large size of *Dikelocephalus* (and some other arthropods from the northern Mississippi Valley) may suggest that these organisms persued *K*-selective stratergies that are associated with stable environmental conditions and high diversity (Gould 1977; Pachut, 1989).

The heterolithic facies preserves a diverse variety of trace fossils (Hughes, 1990) including those made by aglaspidid arthropods (Hesselbo, 1988). The aglaspidid trace *Raaschichnus* was probably formed on the surface of the seabed. In spite of extensive efforts, no traces that might be attributed to trilobites have been found in any facies within the St. Lawrence Formation. The absence of trilobite traces suggests that *Dikelocephalus* did not burrow. This is consistent with the the morphological evidence against burrowing presented above. All available evidence suggests that *Dikelocephalus* was epibenthic.

Great morphological diversity has been demonstrated within *Dikelocephalus* (Hughes, 1990, 1991a,b). Attempts to relate patterns of morphological variation to sedimentological or geographical variations have been unsuccessful. There are no morphological variations which are consistently associated with particular lithotypes and no obvious associations between lithology and morphology exist.

Synecology

A wide variety of invertebrate groups are present in the St. Lawrence Formation, representing a normal Cambrian assemblage (see above). Where abundant aglaspidid arthropods are preserved this reflects favorable taphonomic conditions, rather than indicating a fundamentally different biotic association (Hesselbo, 1987a). The trilobite genera within the St Lawrence Formation represent a unique Upper Cambrian biofacies, which most closely resembles the *Euptychaspis-Eurekia* biofacies of Ludvigsen and Westrop (1982). The diversity of trilobite genera in northern Mississippi Valley deposits from the *Illaenurus* and *Saukia* zones is similar to that in similar aged deposits from the Rocky Mountains of Alberta (Westrop, 1986a). There is no evidence that the northern Mississippi Valley fauna is depauperate compared to that of other north American Upper Cambrian shelf biofacies, although the generic abundance at individual localities is often lower than in other biofacies. Whether this reflects biological factors or differences in taphonomic regime is not known.

Within the St. Lawrence assemblage there is little evidence of the community structure. *Dikelocephalus* was probably subject to predation, and to infestation of its exoskeletal cuticle. The only organism preserved which appears large enough to prey on *Dikelocephalus* is *Dikelocephalus* itself (with the possible exclusion of *Tellerina* and the larger aglaspids). It has been suggested that other large trilobites preyed upon each other (Conway Morris and Jenkins, 1985). When the appendage morphology of trilobites are considered it is not clear how they could have produced the arcuate bites thought characteristic of predator activity. However, there were also large soft-bodied predators (*e.g.* Whittington and Briggs, 1985, on *Anomalocaris*), which may have been responsible.

CONCLUSIONS

Dikelocephalus is found in large numbers at outcrops scattered throughout the northern Mississippi Valley. Although sclerites have suffered some post-molt or post-mortem redistribution, their occurrence reflects the original biological distribution. Preservation is sufficiently good to permit detailed biometric analysis of morphological variation within the genus. Northern Mississippi Valley *Dikelocephalus* is thus a suitable candidate for detailed investigation of growth-related and locality-related morphological variations.

Morphological and geological evidence independently suggest an epibenthic life mode. The gross morphology of *Dikelocephalus* appears conistent with the paleoenvironmental interpretation suggested by sedimentological evidence. Morphological variation and lithology are closely linked in many trilobites (*e.g.* Best, 1961 on *Encrinurus*; Cisne, Molenock and Rabe, 1980 on *Triarthrus*; Cisne *et al.* 1980, 1982 on *Flexicalymene*; Eldredge 1972, on *Phacops*). As northern Mississippi Valley *Dikelocephalus* are very variable, the absence of clear association between morphological and lithological variations is surprising.

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APPENDIX 1

Northern Mississippi Valley occurrence of *Dikelocephalus*

This list includes northern Mississippi Valley localities from which *Dikelocephalus* has been collected. Abbreviations refer to repositories holding relevant material. The locality numbers assigned by previous wokers are included. Abbreviations of localities (in bold type) extend the system introduced by Hesselbo (1987a). A card index detailing the holdings of each museum is deposited at the Geology Museum, University of Wisconsin, Madison.

AMNH: American Museum of Natural History
BMNH: British Museum of Natural History
FMNH: Field Museum of Natural History
LACMIP: Los Angeles County Natural History Museum
(Invertebrate Paleontology)
MPM: Milwaukee Public Museum
SCHSM: Sauk County Historical Society Museum

SMM: Science Museum of Minnesota
UCMP: University of California Museum of Paleontology, Berkeley
UMPC: University of Minnesota (Minneapolis Campus)
USGS: United States Geological Survey (Denver)
USNM: National Museum of Natural History, Smithsonian Institution
UW: University of Wisconsin (Madison) Geology Museum
UW(NH): University of Wisconsin Geology Museum
material collected by Gerald Gunderson and Nigel Hughes

A small collection of *Dikelocephalus* is reposited in the Green Museum, University of Wisconsin, Milwaukee. A representative collection of *Dikelocephalus* from North Freedom has been presented to the Bristol City Museum and to the University of Bristol Geology Department.

Raasch locality numbers prefixed with an 'x' refer to maps stored in the Geology Museum, University of Wisconsin, and at the Milwaukee Public Museum.

TCG refers to Tunnel City Group. SLF refers to St. Lawrence Formation. *Dikelocephalus* is found within two lithofacies within the St. Lawrence Formation; heterolithic and laminated sand lithofacies. These are described in detail in Hughes (1990).

Afton, AN: section alongside west side of Hwy 95, 1 km south of Afton, Washington County., Minnesota. UW (NH). SLF. heterolithic facies.

Arcadia, AAa: quarry on east side of Hwy 93, 4 km south of Arcadia, Trempealeau County, Wisconsin. UW (NH), UW, UMPC. Raasch locality numbers 417.57, x67.6 B19, perhaps also 417.59, x67.51B17, 417.64, 417.68 UMPC locality F206.2. SLF. heterolithic facies.

Arcadia, AAb: section along County Trunk J, 11 km southeast of Arcadia, Trempealeau County, Wisconsin. UW(NH). SLF. heterolthic facies.

Arena, AR: Iowa County, Wisconsin. UW. Raasch locality numbers L381.1 x11.14B6. SLF. heterolithic facies.

Beans Quarry, BQ: near Tunnel City, Monroe County, Wisconsin. UW, MPM, USNM. Raasch locality numbers 139.57, 417.67. USNM site 87E. SLF. laminated sandstone facies.

Bean Hollow, BW: creek on east side of Bean Hollow, Collence School, near Romance, Vernon County, Wisconsin. USNM. Raasch locality number x57.44. TCG. Reno Member.

Black Earth, BE: sections along north side of Hwy 14, 4 km east of Black Earth, Dane County, Wisconsin. MPM. Raasch locality number x11.2. SLF. heterolithic facies.

Black Hawk (Moseman's Farm), BHa: disused quarry, Moseman's Farm, 1 km northwest of Black Hawk, Sauk County, Wisconsin. UW(NH), UW. Raasch locality number x3.78. SLF. heterolithic facies.

Black Hawk (Walster Farm) BHb: exact locality unknown ''1/2 mile south east of quarry on Fingeruth Farm''. south of Honey Creek. Sauk County, Wisconsin. UW. SLF. heterolithic facies.

Boom Hollow, BO: section along west bank of St Croix River, 4 km north of Stillwater, Washington County, Minnesota. UMPC. UMPC locality number F21-14. SLF. heterolithic facies.

Boscobel, BL: section on north side of Hwy 60, behind old brewery, 0.5 km north of Boscobel, Grant County, Wisconsin. MPM. Raasch locality number x54.7. SLF. heterolithic facies.

Button Bluff, LRc: disused quarry above Button Bluff Cemetry, 4 km east of Gotham, above County Trunk JJ, Richland County, Wisconsin. MPM, USNM, UW(NH), UW. Raasch locality number x5.22B6/B18. SLF. heterolithic facies.

Chippewa River Falls, CR: near Chippewa Falls, Chippewa County, Wisconsin. AMNH, FMNH. SLF. heterolithic facies.

Decora Peak, DP: disused quarry on east side of hill, 3 km east of Galesville, Trempealeau County, Wisconsin. UW. SLF. heterolithic facies.

Dellona, DA: about 6 km northeast of Reedsberg. Sauk County, Wisconsin. UW. Raasch locality number x12.93. SLF. heterolithic facies.

Dresbach, DH: exact locality unknown Winnona County, Minnesota. UW. SLF. heterolithic facies.

Eagle Cave, EC: Quarry on east side of Eagle Cave Road, 2 km north of intersection with Hwy 60, Richland County. Wisconsin. UW(NH). SLF. heterolithic facies.

Eleva, EA: 4.5 km northeast of Eleva, Eau Claire County, Wisconsin. MPM, USNM. USNM site 86o. SLF. laminated sandstone facies.

Excelsior, Sauk County, ER: exact locality unknown, near town of Excelsior, Sauk County, Wisconsin. UW. SLF. heterolithic facies.

Excelsior, Richland County, EX: road cut on east side of County Trunk F, about 3 km. north of Excelsior, Richland County, Wisconsin. UW(NH). TCG. Uppermost Reno Member.

Freeburg, FG: exposure alongside gravel road, 1 mile west of town, near abandoned railroad bridge, Freeburg, Houston County, Minnesota. UMPC, UW(NH). TCG. Uppermost Reno Member.

Galesville, GE: temporary exposure found by road workers, Hwy 35. 1 km west of Galesville, Trempealeau County, Wisconsin. UW. SLF. heterolithic facies.

Gays Mills, GM: extended road cut, north side of Hwy 171, about 1.5 km east of Gays Mills, Crawford County, Wisconsin. UW(NH). SLF. heterolithic facies.

Genoa, GA: NE1/4 NE1/4 Sec 28 T13N R7N road cut near Genoa, Hwy 56, Vernon County Wisconsin. MPM. Raasch locality number x57.22B1/15. TCG. Uppermost Reno Member.

Gibralter Bluff, LG: SW1/4 SE1/4 Sec 18 T10N R8E also known as Van Ness Quarry, Columbia County, Wisconsin. MPM, USNM, UW. Raasch locality number x 1.10 USNM site 86. Also see note for Lodi C. SLF. heterolithic facies.

Gotham A, LRe: 2.5 km east of Gotham, Richland County, Wisconsin. MPM, USNM. Raasch locality number x 5.18. SLF. heterolithic facies.

Gotham B, LRd: SE1/4 Sec 27 T9N R2E, 3 km east of Gotham, Richland County, Wisconsin. MPM, USNM. Raasch locality number x5.11B11/12. SLF. heterolithic facies.

Grandview School, GS: near Stoddard, Vernon County, Wisconsin. USNM Raasch locality number x 57.8 B2. TCG. Uppermost Reno Member.

Hell Hollow, HW: SE1/4 Sec 23 T10N R4W side of HWY 26,1.8 km north of Reno, Houston County, Minnesota. UMPC. UMPC locality number F57.6B. TCG. Uppermost Reno Member.

Hillside, SG: 1.5 km northeast of Hillside, 3 km south of Spring Green. Iowa County, Wisconsin. MPM, USNM. Raasch locality number x 5.4i. SLF. heterolithic facies.

Hogsback Hill, HL: Clifton, north of Kendall, Monroe County, Wisconsin. MPM. Raasch locality number x 25.183. SLF. laminated sandstone facies.

Hokah, HH: known as Whitman's Quarry, on Mt Hope, thought to be near old railroad embankment, Houston County, Minnesota. UPMC, FMNH. SLF. heterolithic facies.

Houlton, HN: exact locality unknown, opposite Stillwater, on bank of St Croix River, St Croix County, Wisconsin. UMPC. SLF. heterolithic facies.

Kingston, KN: 1.5 km south of Kingston, Green Lake County, Wisconsin. UW. Raasch locality numbers L118.1, x 111.1. SLF. heterolithic facies.

LaGrange Mountain, RWa: also known as Barn Bluff, east side of Hwy 61. in town of Redwing, Goodhue County, Minnesota. UMPC, AMNH, FMNH, MPM, USNM. USNM site 113. SLF. heterolithic facies.

Lake City, LC: in small quarry, 3 km north west of Lake City, Wabesha County, Minnesota. USNM. USNM site 132. SLF. heterolithic facies.

Lansing, LSa: road cuts on west side of Hwy 26, 0.5—1 km north of town of Lansing, Allamakee County, Iowa. UW (NH), USNM. USNM site 86B. TCG. Uppermost Reno Member. SLF. heterolithic facies.

Lansing, LSa,b: 80 metres west of road, 3 km south of Lansing on Hwy 26. Allamakee County, Iowa FMNH, UW, USNM. USNM site 66B, Raasch locality number 128x. TCG. Uppermost Reno Member.

Lindina, LA: exact locality unknown, near Goodenough Hill, Juneau County, Wisconsin. USNM. Raasch locality number x 24.8. Also see Mauston Quadrangle. SLF. laminated sandstone facies.

Lodi, LIa: in small quarry on small rounded hill. NW¼ SW¼ Sec 6, T 9 N, R 8 E, 6 km southwest of Lodi, Dane County, Wisconsin. USNM. USNM site 87i. SLF. heterolithic facies.

Lodi, LIb: exact locality unknown. Lodi. USNM. USNM site 87k. SLF. heterolithic facies.

Lodi, LG: see note for Gilbalter Bluff. Apparently specimens from the two localities became mixed at the USNM. SLF. heterolithic facies.

Lone Rock, LRa: on Hwy 130 4.5 km north of railroad station in Lone Rock. SW 1/4 SW1/4, Sec 25, T9N. R2E. Richland County, Wisconsin. MPM, USNM. Raasch locality number x5.20B18. SLF. heterolithic facies.

Lucas, MT: quarry on south side of Hwy 29, 0.25 km east of junction with County Trunk Q, 0.1 km west of junction with Gales Road. About 14 km west of Memomonie, Dunn County, Wisconsin. SE¼ Sec 29 T28N R4W. 2 fossiliferous horizons. UW(NH), UW. Rassch locality numbers x 87.1y,x 417.55, 417.63, 140.26. SLF. heterolithic facies.

Madison, MS: locality unknown, presumably within Madison (perhaps at Maple Bluff?), Wisconsin. AMNH, UW. SLF.

Maiden Rock, MR: road cuts on east side of Hwy 35, opposite Maiden Rock Memorial carpark, 5 km south of Maiden Rock town. Pepin County, Wisconsin. UW(NH). SLF. heterolithic facies.

Mapple Bluff, MB: east shore of Lake Mendota, Madison, Wisconsin. UW. SLF.

Marine, ME: Median Lake, 1.5 km north of Marine-on-St Croix, Washington County, Minnesota. UPMC, UMPC locality number F28.14N. SLF. laminated sandstone facies.

Mauston Quadrangle, MN: Several specimens from unspecified localities near Goodenough Hill, Juneau County, Wisconsin. UW, USNM. Raasch locality numbers x 24.8, 115.1. SLF. laminated sandstone facies.

Mazomanie, MMa: Bluffs and old quarry above town NE¼ NE¼ Sec 21 T8N R6E. Dane County, Wisconsin. Section described in detail by Hesselbo (1987a) UW, UCMP, LACMIP, AMNH, MPM, USNM, BMNH. Raasch locality number x11.1 USNM site 85x. SLF. heterolithic facies.

Mindoro, MD: exact locality unknown, near Mindoro. La Cross County, Wisconsin. MPM. Raasch locality number x58.4. SLF. heterolithic facies.

Minneiska, MA: Mississippi River banks at Wabesha—Winona County line, Minnesota. USNM. Possibly USNM site 99, though this listed as Franconian. SLF. heterolithic facies.

Mondovi, MI: exact locality unknown, listed as Thompson's Valley, Buffalo County, Wisconsin. MPM. SLF. heterolithic facies.

Mormon Coulee, MU: 4 km north of Coon Valley, La Cross County, Wisconsin. UW. Raasch locality number x 57.101. SLF. heterolithic facies.

Mound Ridge, MO: Bluffs overlooking Mississippi River, 2.5 km west of Mound Ridge School, Vernon County, Wisconsin. USNM. Raasch locality number x 57.32. TCG. Uppermost Reno Member.

Muscoda, MCa: Hickory Flat Road quarries. Hickory Flat Road. 2 km southeast of junction with Sand Branch Road, 5 km south of Muscoda, Grant County, Wisconsin. Section described in detail by Hesselbo (1987a) UW(NH). SLF. heterolithic facies.

Muscoda, MCb: Sand Branch Road Quarry. About 0.5 km east of Junction with County Trunk G, 4 km southwest of Muscoda, Grant County, Wisconsin. Section described in detail by Hesselbo (1987a) MPM, UW(NH). SLF. heterolithic facies.

Myers Hill, MY: north side of County Trunk A, 1 km east of Clifton, Monroe County, Wisconsin. MPM, USNM. Raasch locality number x 25.194 B1 USNM site 89n. SLF. laminated sandstone facies.

Netwon, NNa: east side of County Trunk O, 1 km north east of Netwon School (now demolished) Vernon County, Wisconsin. Locality no longer exposed. UW, Raasch locality number x 57.59. TCG. Uppermost Reno Member.

Newton, NNb: north fork of Bad Axe River, NE 1 / 4 SE 1/4 Sec 27, T13N R6W, Vernon County, Wisconsin. UW. Raasch locality numbers x 57.62B2, L141.26. TCG. Uppermost Reno Member.

North Freedom, NF (NFB2 & NFB8): quarry on west side of Mirror Lake road, 0.5 km north of intersection with Hwy 136, 4 km north northeast of North Freedom, Sauk County, Wisconsin. Now infilled. Also known as ''Rock Springs''. UMPC, MPM, UW, FMNH, UW(NH), USGS. Raasch locality number x3.65, L138.1. Old quarry at equivalent horizon on east side of road now infilled. SLF. heterolithic facies.

Oak Hill, OH: quarry on east side of County Trunk FF, 0.5 km northeast of Oak Hill School, Buffalo County, Wisconsin. LACMIP. UW(NH). SLF. heterolithic facies.

Ontario, OO: exact locality unknown, near Ontario, Vernon County, Wisconsin. MPM. Raasch locality number x 16.1, SLF. heterolithic facies.

Osceola, OA: Cascade Falls section on Mill Creek, and Eagle Point Bluff, south end of town of Osceola and roadcuts along HWY 243, Polk County, Wisconsin. UMPC, MPM, USNM, UW(NH), LACMIP. SLF. heterolithic facies.

Osceola, OB: road cuts at Osceola Bridge during construction. Osceola Town, Polk County, Wisconsin. UMPC. UMPC locality number F34a.4N, SLF. laminated sandstone facies.

Paunocks Quarry, MQ: ''west of Madison'', presumed within capital district. UW. SLF. heterolithic facies.

Point Jude, LRb: NE¼ Sec 34, T9N R2E. Bluff 0.5 km north of County Trunk JJ, 5 km west of Gotham, Richland County, Wisconsin. MPM, UW. Raasch locality number x 5.21 B13. SLF. heterolithic facies.

Pleasant Branch, MP: Quarry on High Road, Middleton, Capital District. Madison, Dane County, Wisconsin. MPM. Raasch locality number x 4.21. SLF.

Praire du Sac, SPb: NE ¼ NE ¼ Sec 31 T10N R6E, old quarry in woods above intersection of Praire Road and Swiss Valley Road, Sauk County, Wisconsin. Section described in detail by Hesselbo (1987a) MPM, SCHSM, FMNH, USGS, USNM, UW, UW(NH). USNM sites 85 and 85s. Raasch locality number x3.10. SLF. heterolithic facies.

Reeds Landing, RL: Bluffs 3 km north of Reeds Landing, Wabesha County, Minnesota. UMPC, FMNH, USNM. USNM site 97. SLF. heterolithic facies.

Reedsburg, RG: quarry on west side of County Trunk H, 4 km northeast of Reedsburg, Sauk County, Wisconsin. USNM, MPM. TCG. Uppermost Mazomaine Formation.

Richland Center, RCa: NW ¼ SE ¼ Sec 21 T10N R1E. Bluffs on east side of town, Richland County, Wisconsin. No longer exposed. MPM, USNM, UW. Raasch locality number x 5.7 B6. SLF. heterolithic facies.

Richland Center, RCc: bluffs 0.75 km southwest of Richland Center. Richland County, Wisconsin. UW. Raasch locality number x5.17. SLF. heterolithic facies.

Richland Center, RCd: bluffs on east side of town, 200 metres south of RCa. Richland County, Wisconsin. MPM, USNM. Raasch locality number x 5.8B6. SLF. heterolithic facies.

Richland Center, RCe: bluffs 0.75 km west of town centre, Richland County, Wisconsin. MPM, USNM Raasch locality number x5.31. SLF. heterolithic facies.

Ridgeland, RD: approaching top of hill on east side of Hwy 25, just south of Elm Lane, recorded as ''Wilson Twp'', Ridgeland, Dunn County, Wisconsin. UMPC, UW. Raasch locality number 401.1B8. UMPC locality number F45.9. SLF. heterolithic facies.

Rocky Hill, RH: roadcut along side of Preuss Road, 3 km southeast of site of old Rocky Hill school. 6 km northeast of Glendale, Juneau County, Wisconsin. MPM Raasch locality number x 25.111. SLF. heterolithic facies.

Sauk Praire, SPa: bluffs on east side of Wisconsin River, above Hwy 188 overlooking Sauk City. Dane County, Wisconsin. Section described in detail by Hesselbo (1987a). Sauk County, Wisconsin. FMNH, UW(NH). SLF. heterolithic facies.

Sauk City, SC: exact locality unknown, Dane County, Wisconsin. FMNH. SLF. heterolithic facies.

Spring Green, SG: also known as Hillside, road cut on west side of Hwy 22. 3 km south of Spring Green, Iowa County, Wisconsin. MPM. Raasch locality number x 5.4. SLF. heterolithic facies.

Spring Green, SRa: Disused quarry and old roadcuts, no longer exposed, on side of Hwy 23, 4 km north of railroad station, Spring Green, Sauk County, Wisconsin. Also known as Guy Ryman's quarry. NE¼ SE¼ Sec 36 T8N R3E. UW, MPM, USNM, FMNH, Raasch locality number x 5.23B11. SLF. heterolithic facies.

Stillwater (Fairy Glen), SWa: section no longer exposed, at Fairy Falls, Fairy Glen, just north of intersection of Hwy 36 and Hwy 95, 1.5 km north of Stillwater, Washington County, Minnesota. Collections mostly come from about 10 metres above the base of the St Lawrence Formation. Type locality. UMPC, LACMIP, AMNH, MPM, USNM. USNM site 85b, UMPC locality number F21. SLF. heterolithic facies.

Stillwater, SWb: section no longer exposed, road cut made during construction of Hwy 95, 0.5 km north of Stillwater, just north of old prison, Washington County, Minnesota. Collection made from heterolithic beds just below Norwalk Member by Dr J.C. Ferguson. SMM. SLF. heterolithic facies.

Stockton Hill, SH: roadcuts along Hwy 14, west of Stockton, Winona county, Minnesota. UMPC. SLF. heterolithic facies.

St Lawrence, SL: section along Minnesota River, 1 km north of Belle Plaine, Scott County, Minnesota. UMPC, UW. SLF. heterolithic facies.

Swain Hollow, SN: 4.5 km north of Chaseburg, Vernon County, Wisconsin. UW. Raasch locality numbers x57.87, 141.34. SLF. heterolithic facies.

Trempealeau, TU: section on promontory jutting into Mississippi River, 2 km south of Trempealeau, Trempealeau County, Wisconsin. UMPC, AMNH, USNM, MPM. USNM site numbers 83,3 and 83,2, also 135d. SLF. heterolithic facies.

Tunnel Hill, TH: section also known as ''Kendall'', east end of Tunnel No 1 on Elroy—Sparta trail, off Hwy 71, about 3 km west of Kendall, Monroe County, Wisconsin. MPM, USNM. Raasch locality number x 25.46B5, USNM site 86i. SLF. laminated sandstone facies.

Victory, VY: section on bluff overlooking Mississippi River, directly east of Minnesota/Iowa border line, SW 1/4, NE¼ Sec 12 T12N R7W. Vernon county, Wisconsin. UW, USNM. Raasch locality numbers x 57.36B45, L141.25/L141.27. SLF. heterolithic facies.

Weston, WN: exact locality unknown, near Weston—10 km south east of Menomonie, Dunn County, Wisconsin. MPM. Raasch locality number 150.0. SLF. heterolithic facies.

Wilton, WTa,b: east end of Tunnel No 2 on Elroy—Sparta trail, off Hwy 71, 2.5 km west of Wilton, Monroe County, Wisconsin. FMNH, MPM, UW. Raasch locality number 139.53, 371.22, x 52.10B18, 417.62/418.1. USNM site 87f. SLF. laminated sandstone facies.

Winona, WI: exact locality unknown, near town of Winona, Winona County, Minnesota. Collected by Stauffer. UMPC. possibly UMPC locality F10.3X. TCG. Uppermost Reno Member.

Wood Hill, WH: NE¼ NE¼ Sec 10 T 15N R2E. west side of Hwy 80, about 5 km southwest of New Lisbon, Juneau County, Wisconsin. Also known as Johnson Hill (for locality on east side of Hwy 80). UW, MPM. Raasch locality numbers 115.7, x 24.9B65. SLF. heterolithic facies.

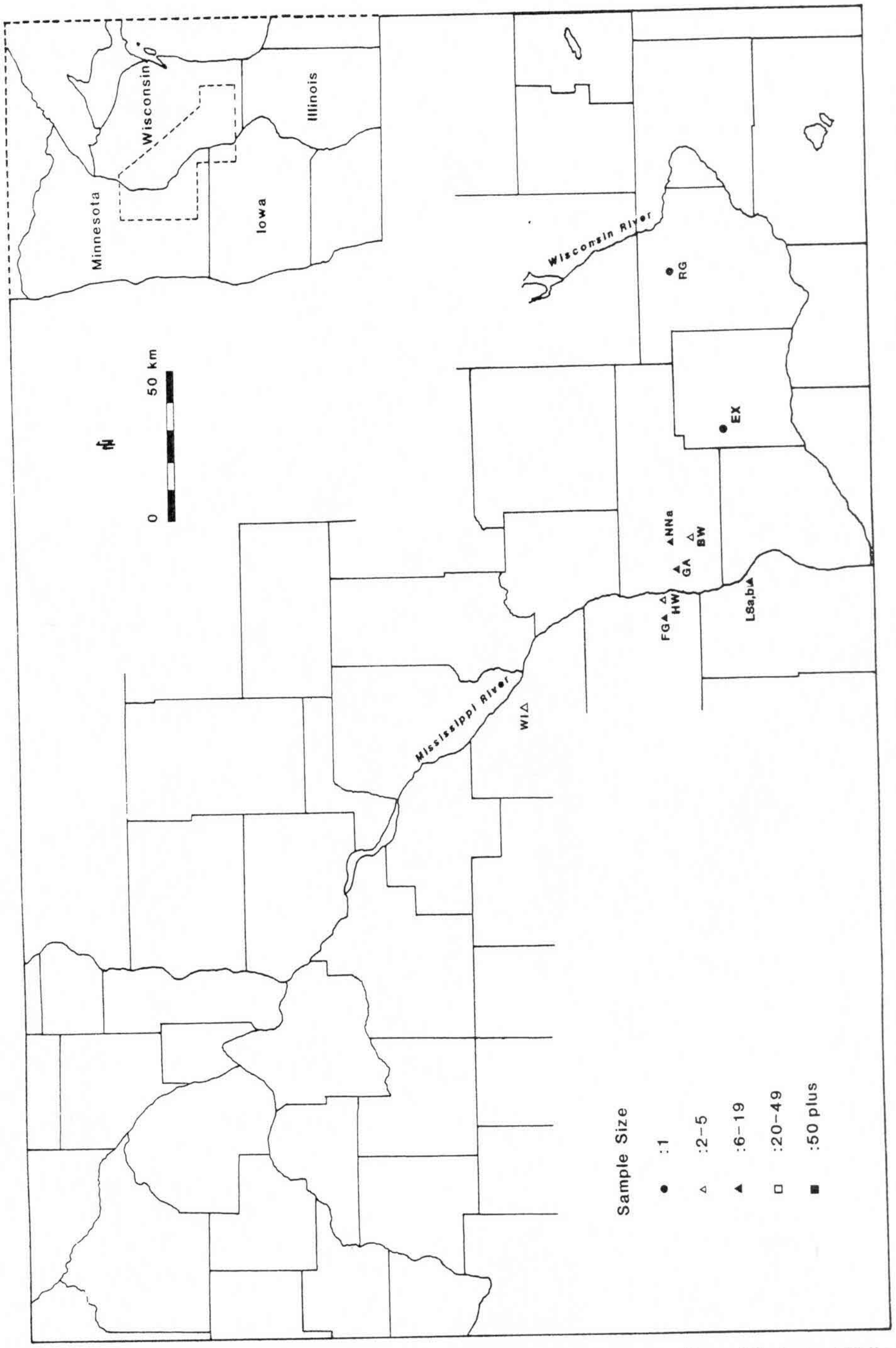


Fig. 1. Distribution of *Dikelocephalus* within the Tunnel City Group, northern Mississippi Valley. See Appendix 1 for locality details. Approximate outcrop area of northern Mississippi Valley Cambrian deposits shown in the top right.

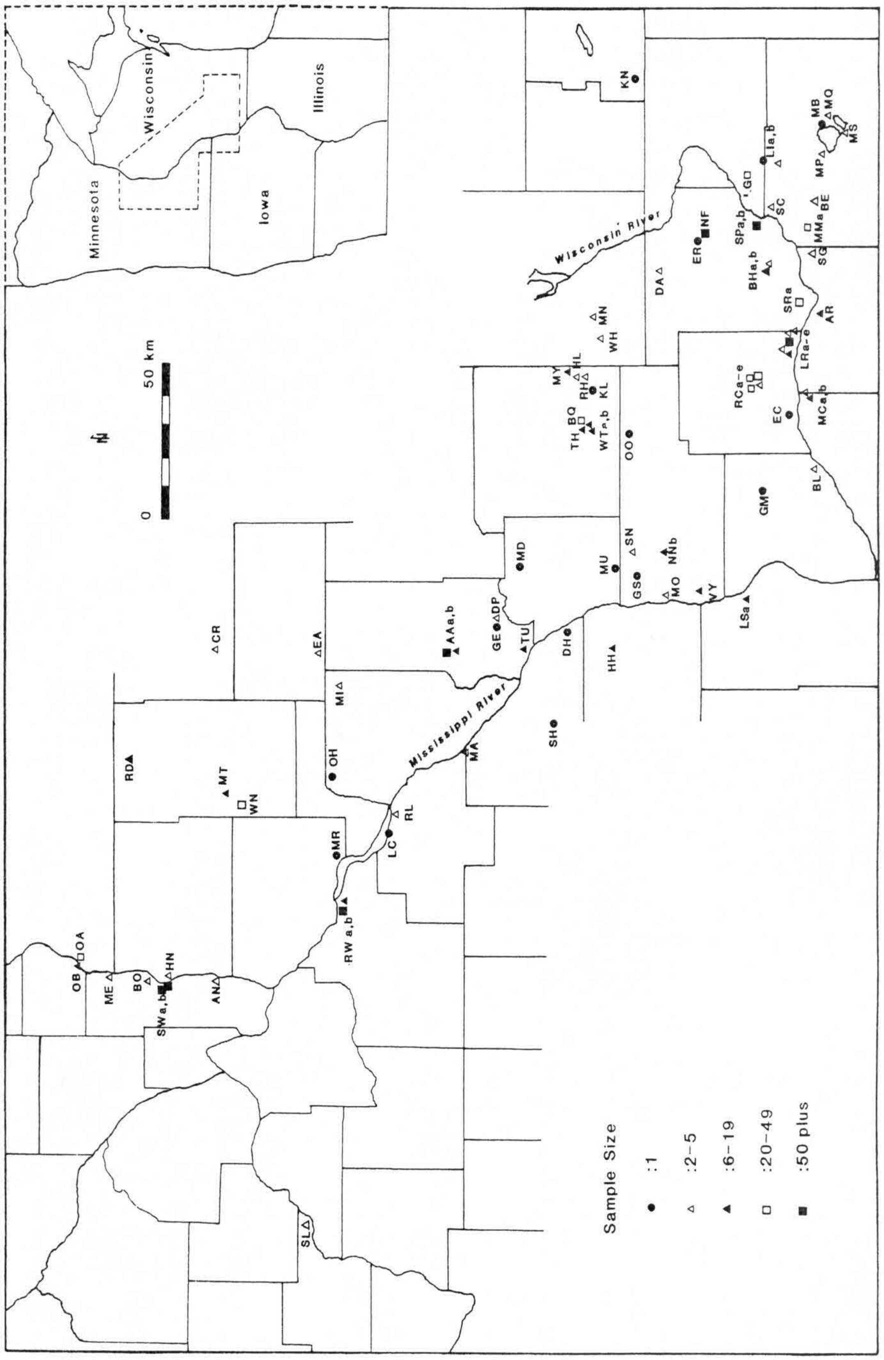


Fig. 2. Distribution of *Dikelocephalus* within the St. Lawrence Formation, northern Mississippi Valley. See Appendix 1 for locality details. Approximate outcrop area of northern Mississippi Valley Cambrian deposits is shown in the top right.

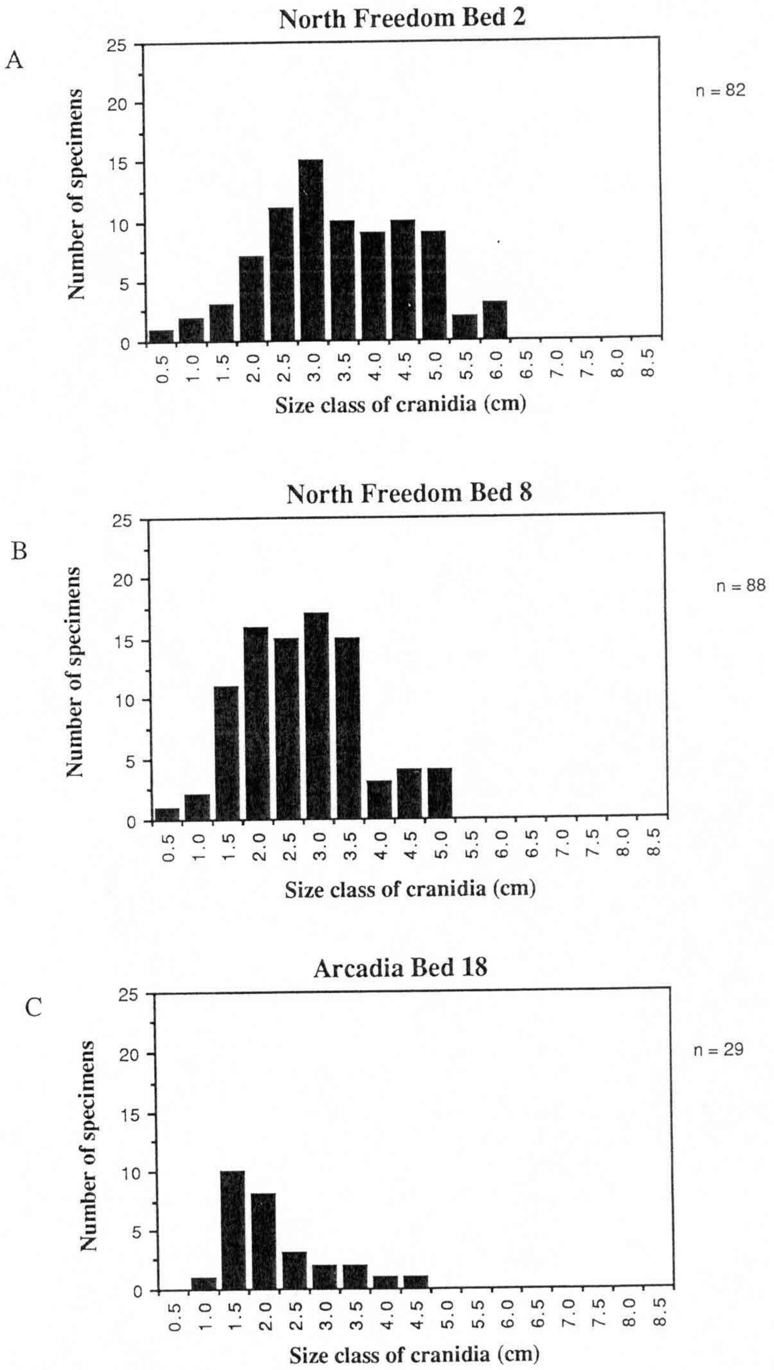
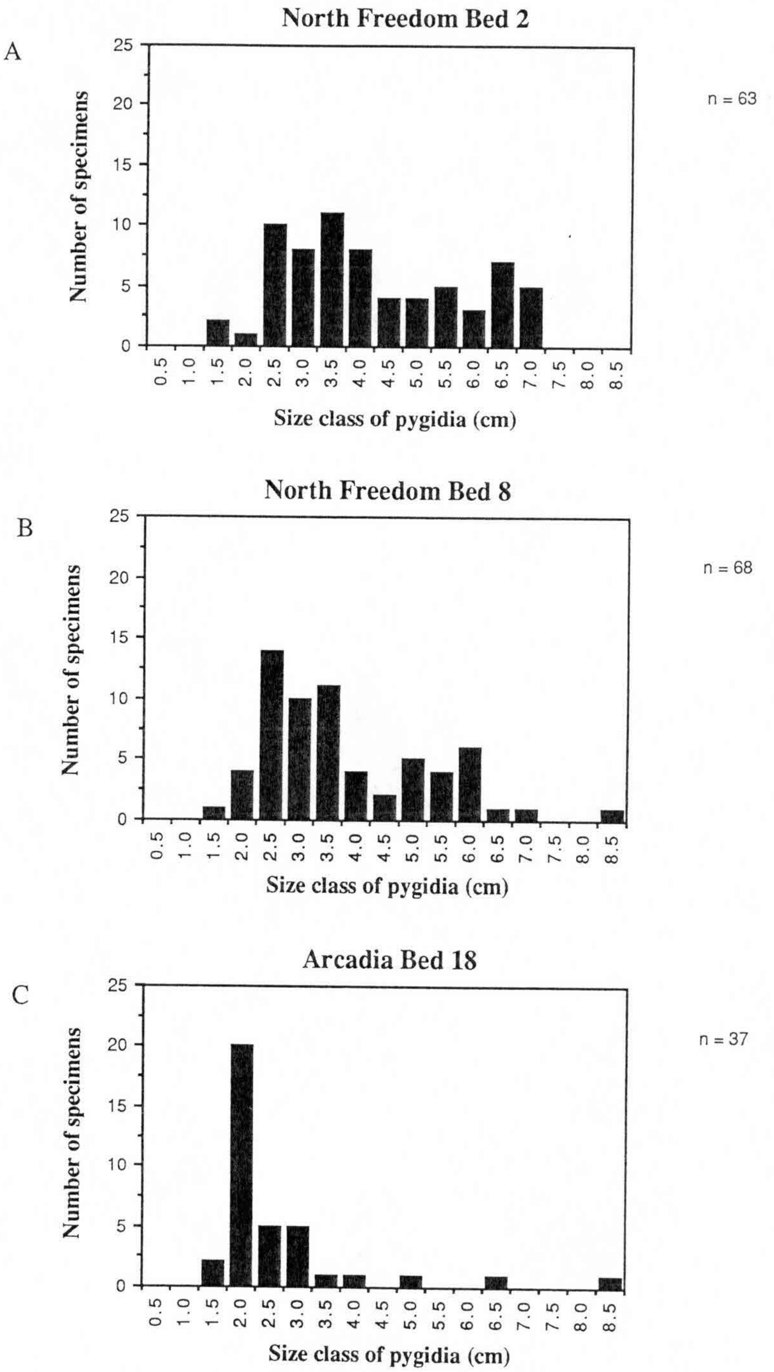


Fig. 3. Size distribution of *Dikelocephalus* cranidia from three localities. Size classes represent 0.49 cm intervals (i.e. the first class includes cranidia between 0 - 0.49 cm). See Appendix 1 for locality details.



ig. 4. Size distribution of *Dikelocephalus* pygidia from the same three localities. Size classes present 0.49 cm intervals (i.e. the first class includes pygidia between 0-0.49 cm). See Apndix 1 for locality details.

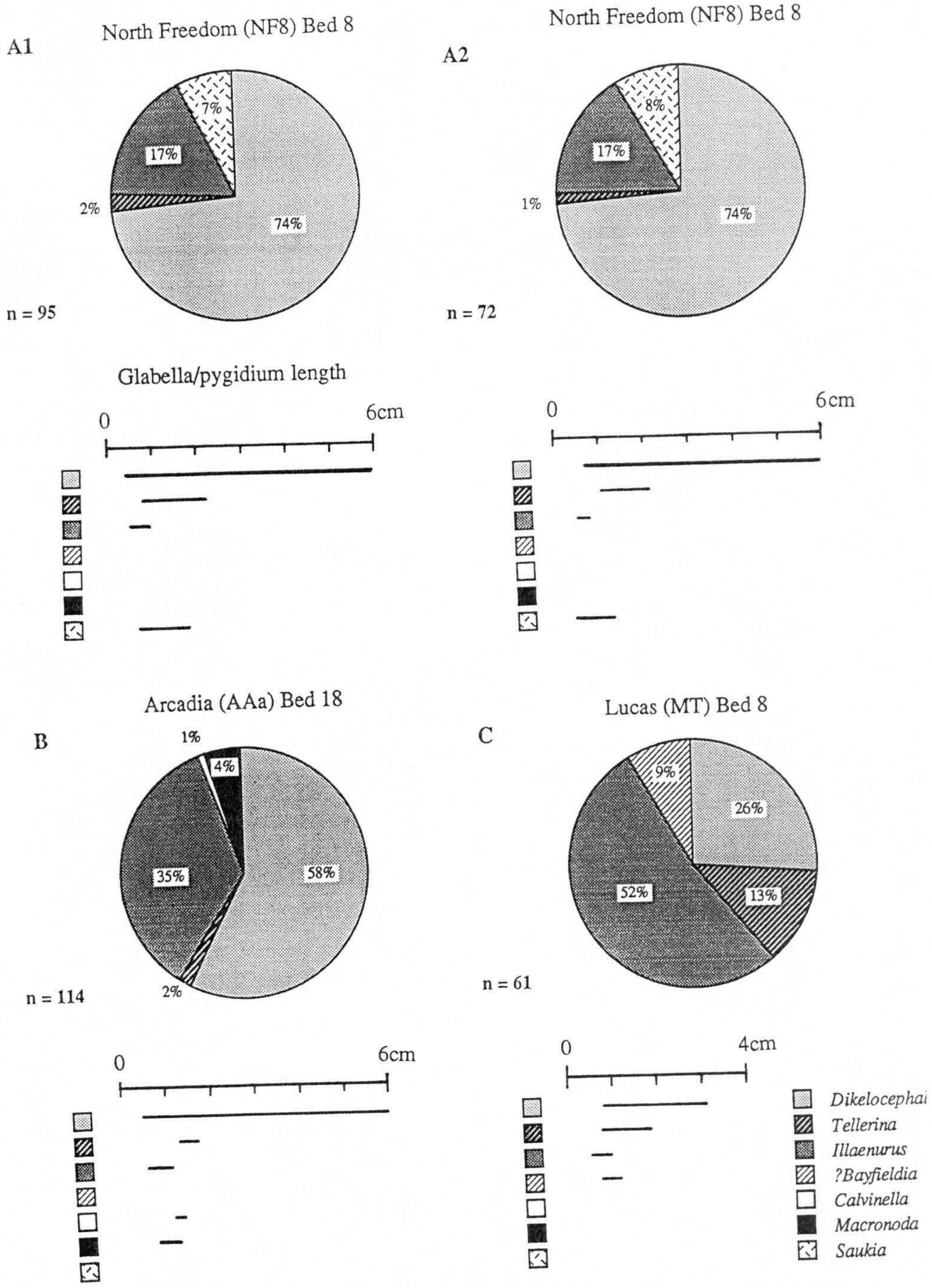
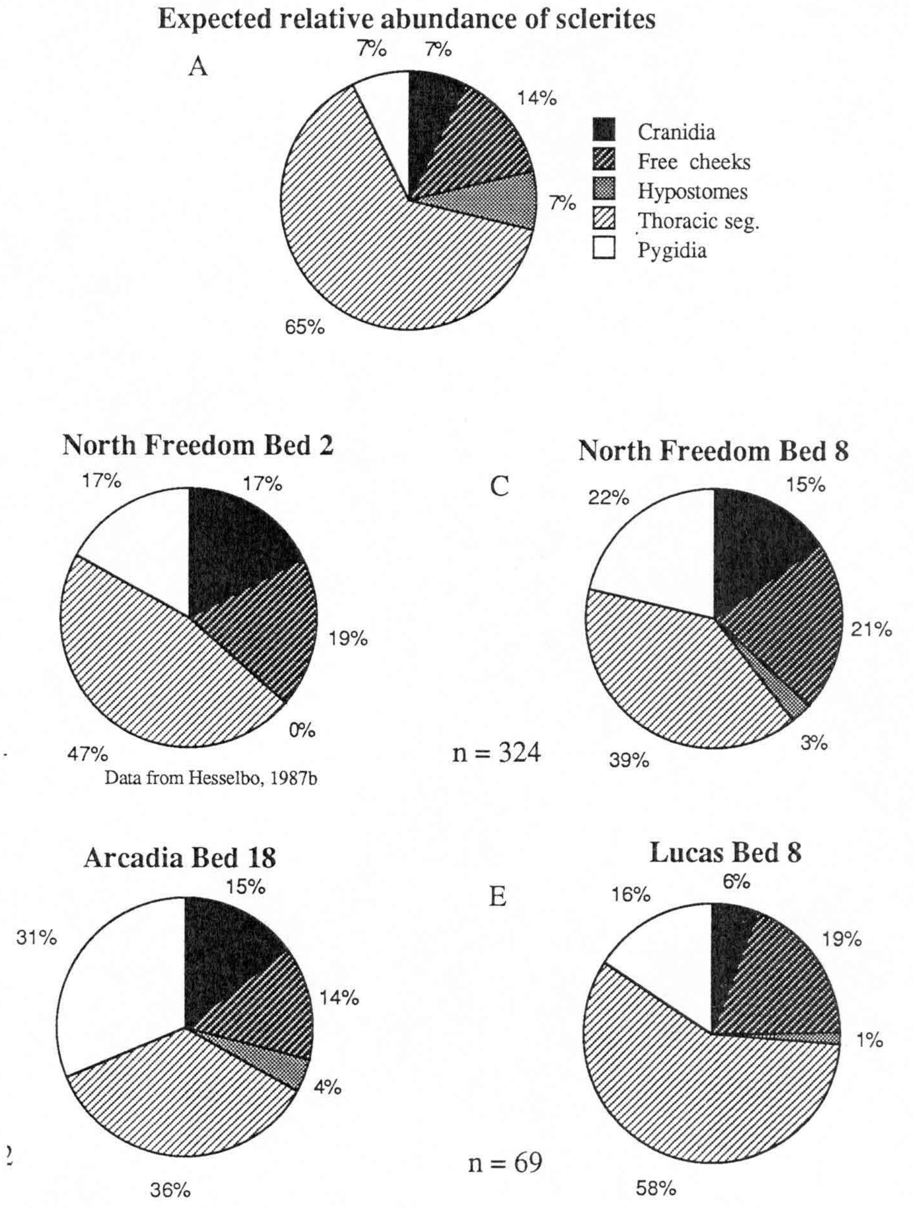
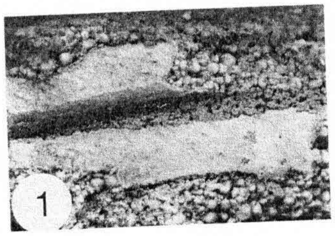


Fig. 5. Generic relative abundances and size ranges of cranidia and pygidia from four localities within the St. Lawrence Formation. The collections from North Freedom Bed 8 (A1 and A2) were made 20 metres apart. See Appendix 1 for locality details.



ig. **6.** Relative abundance of *Dikelocephalus* sclerites from four localities within the St. awrence Formation.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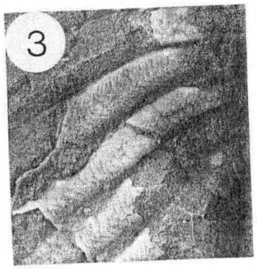
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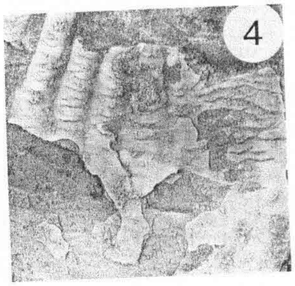
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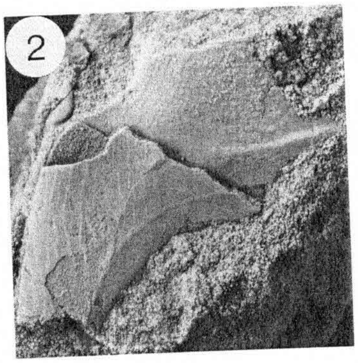
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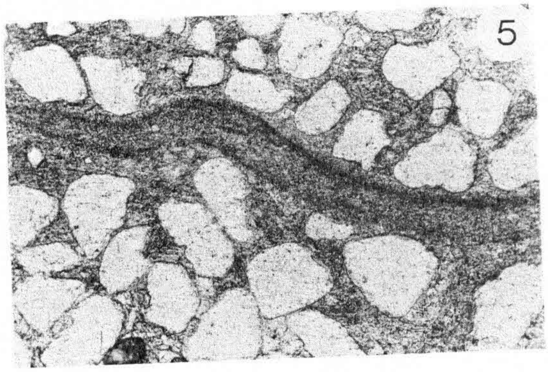
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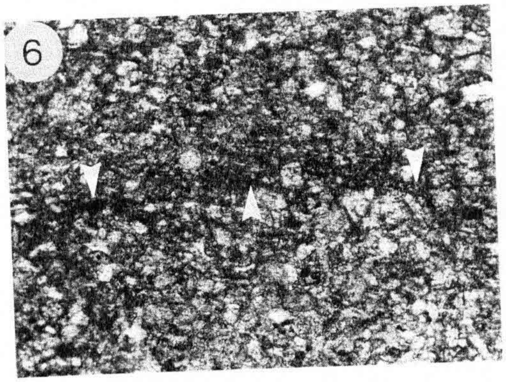
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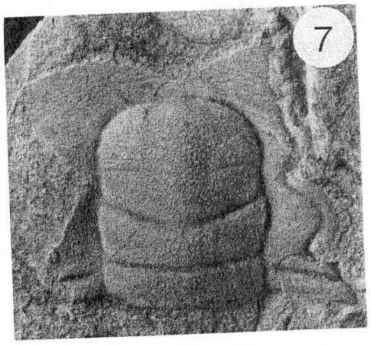
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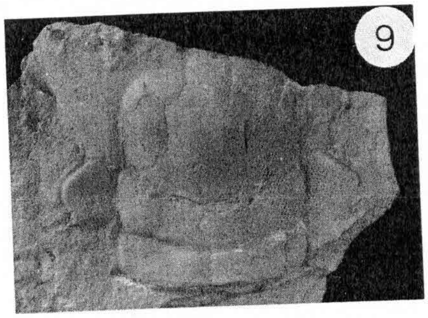
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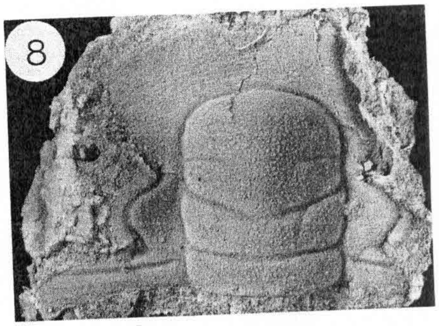
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Plate 1

All material illustrated in plates belongs to *Dikelocephalus*. All specimens are from the St. Lawrence Formation unless otherwise stated. Repository abbreviations are explained in Appendix 1.

Fig. 1. UMPC9408c. Cuticle of thoracic segment. Van Oser-Member. Osceola (OA), x 2.

Fig. 2. AMNH44021. Ventral surface of free cheek, cuticle preserved. Van Oser Member. ''Menomonie River'', Wisconsin. x 1.5.

Fig. 3. AMNH44022. Cuticle of pygidium. Fairy Glen, Stillwater (SWa), x 1.5.

Fig. 4. AMNH44022. Cuticle of pygidium. Fairy Glen, Stillwater (SWa), x 1.5.

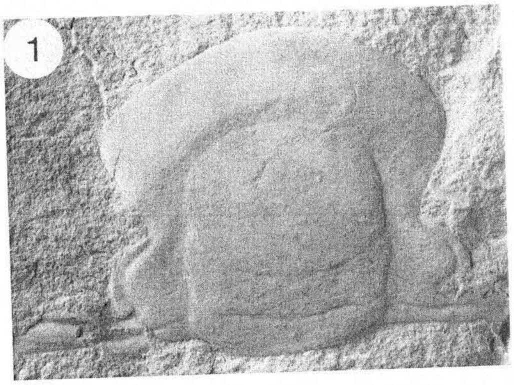
Fig. 5. AMNH44021. Thin section of cuticle. Van Oser Member. Large grains are quartz, matrix is dolomite.''Menomonie River'', Wisconsin. Plane polarized light. x 8.

Fig. 6. Thin section of composite mold. Matrix grains are euhedral dolomite rhombs (planar-E texture). Dark material is illite. North Freedom Bed 2 (NF). Arrows mark position of mold. Crossed polars. x 40.

Fig. 7. UW4006-17a. Cranidium, internal mold showing pustulation and terracing on frontal area. North Freedom Bed 8 (NF). x 2.

Fig. 8. UW4006-17b. Latex cast of external mold of cranidium illustrated above, showing pustulation and terracing on frontal area. North Freedom Bed 8 (NF). x 2.

Fig. 9. UW4006-240. Cranidium showing sagittal crack and polygonal cracks. North Freedom Bed 2 (NF). x 0.5.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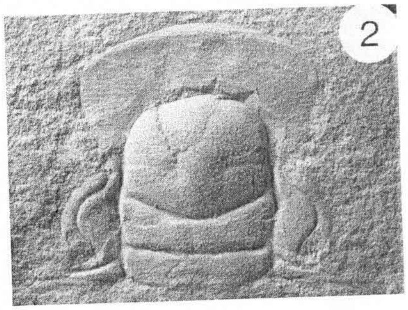
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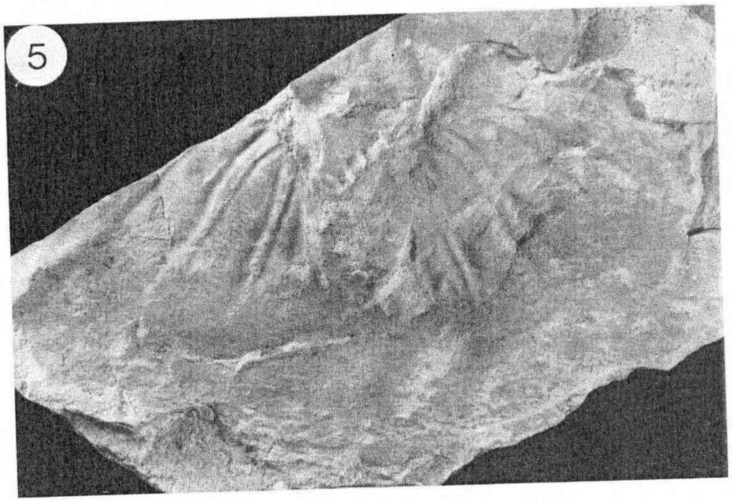
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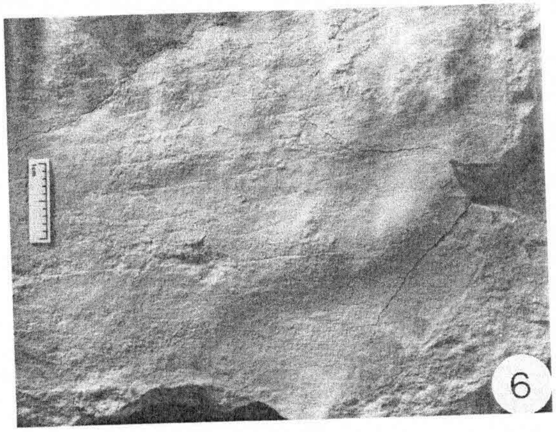
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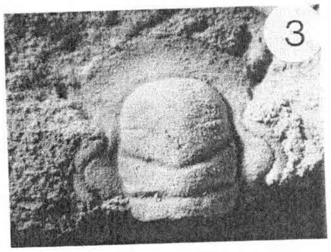
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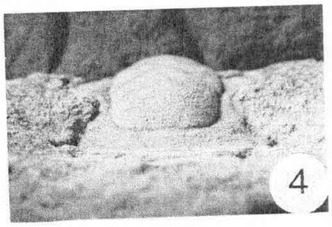
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Plate 2

Fig. 1. UW4006-338. Cranidium showing plastic deformation. Arcadia Bed 18 (AAa). x 1.

Fig. 2. UW4006-293. Fractured cranidium. Arcadia Bed 18 (AAa). x 1.5.

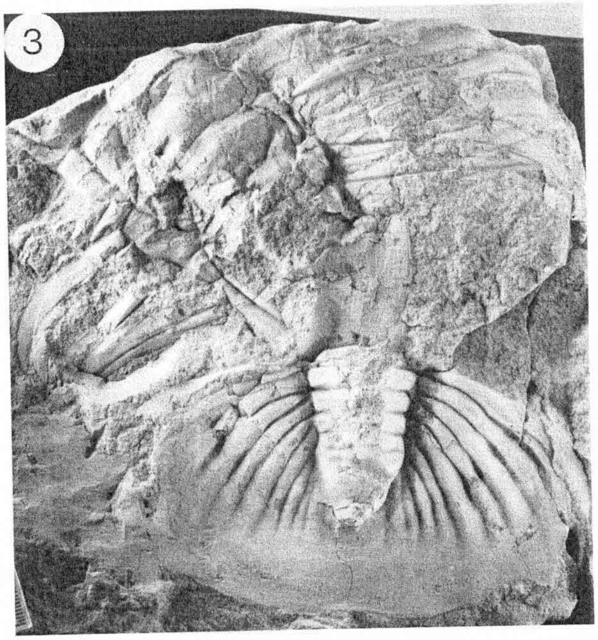
Fig. 3. UMPC6605a. Cranidium preserved in laminated sandstones. Figured by Nelson (1951, pl. 110, fig. 13). Marine (ME). x 2.

Fig. 4. UMPC6605a. Anterior view of cranidium figured above. x 2.

Fig. 5. UW4006-374. Large pygidium showing warping. Muscoda (MCa). x 0.3.

Fig. 6. UW4006-374. Detail of pygidium figured above.

Fig. 7. UW4006-438. Tip of large thoracic segment showing petaloid facet and longitudinal vental terracing. Black Hawk (BHa). x 0.5.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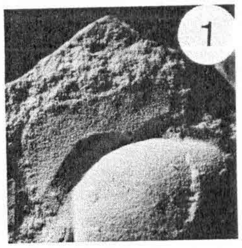
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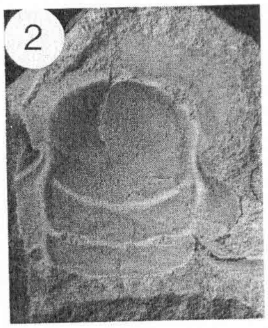
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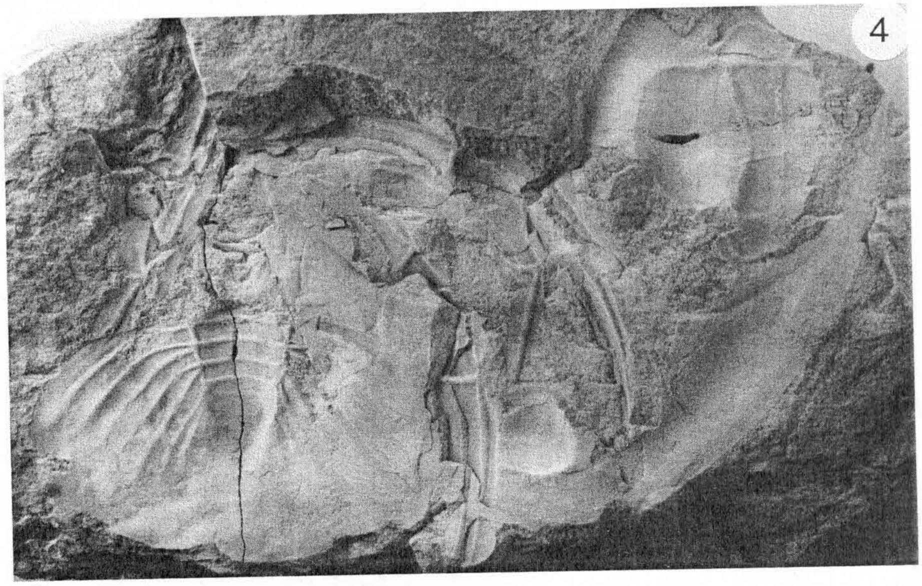
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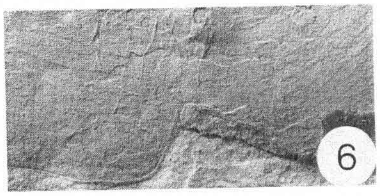
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Plate 3

Fig. 1. AMNH39088a. Original cranidium of *Dikelocephalus minnesotensis* var. Hall (1863). Frontal area fractured along anterior border. LaGrange Mountain (RWa). x 2.

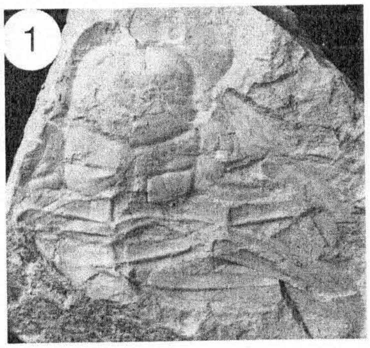
Fig. 2. AMNH39088b. External mold of cranidium figured above, showing fractured anterior border. LaGrange Mountain (RWa). x 1.5.

Fig. 3. USNM443594. Sclerite association. Mazomanie (MMa). x 0.5.

Fig. 4. USNM443595. Sclerite association. Locality unknown. x 1.

Fig. 5. UW4006-82. Pygidium showing teretology on pleural platform. North Freedom Bed 2 (NF). x 0.5.

Fig. 6. UW4006-191. Counterpart of pygidium, showing broken posterior margin with marginal rim. North Freedom Bed 2 (NF). x 1.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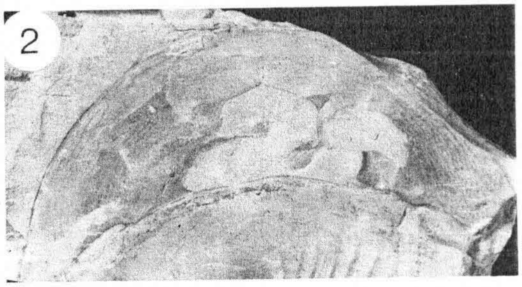
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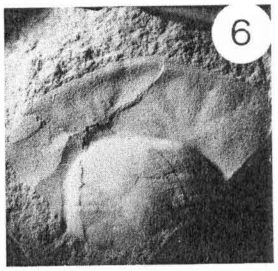
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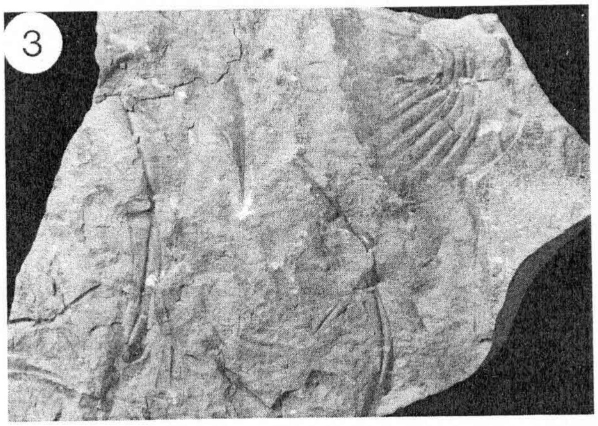
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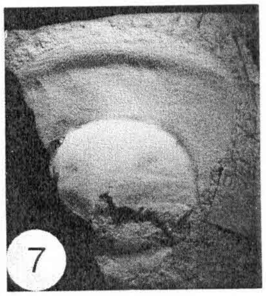
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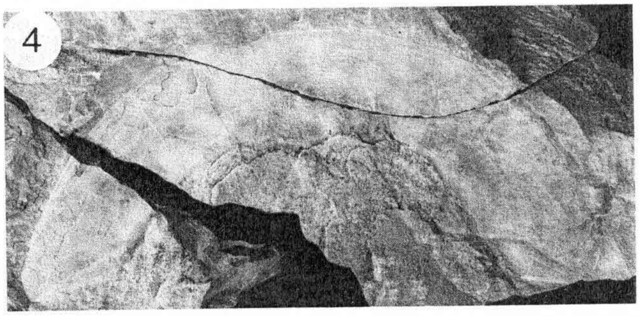
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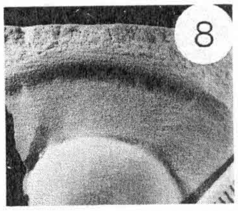
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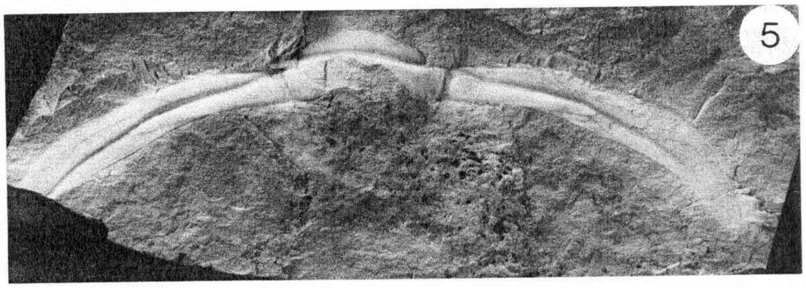
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Plate 4

Fig. 1. UW4006-414. Association of disarticulated cranidium and thoracic segments. North Freedom Bed 2 (NF). x 0.5.

Fig. 2. UW4006-146. Yoked free cheeks and pygidium counterpart. North Freedom Bed 2 (NF). x 0.5.

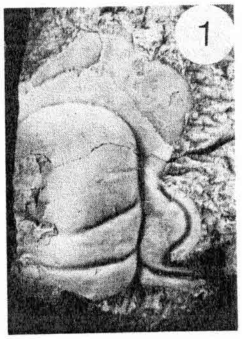
Fig. 3. UW4006-128. Distribution of sclerites on bedding surface. North Freedom Bed 2 (NF). x 0.5.

Fig. 4. UW4006-375. Yoked free cheeks. Muscoda (MCa). x 0.3.

Fig. 5. UW4006-438. Large thoracic segment showing petaloid facet and longitudinal ventral terracing. Black Hawk (BHa). x 0.5.

Fig. 6. USNM443596. Anterior of cranidium showing caeca. LaGrange Mountain (RWa). x 1.5.

Fig. 7 & 8. AMNH39082. Anterior of cranidium showing caeca. Original of *Dikelocephalus minnesotensis* var. *limbatus* Hall, 1863. LaGrange Mountain (RWa). x 1.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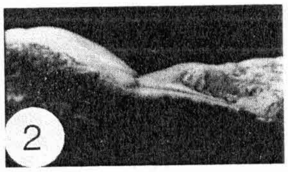
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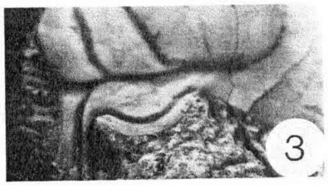
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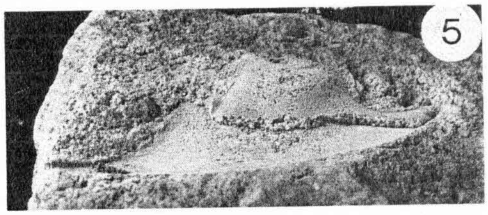
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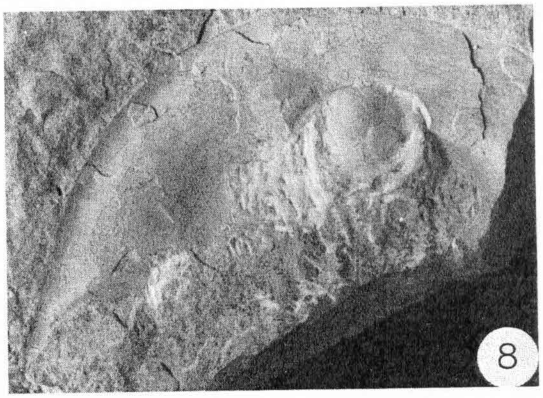
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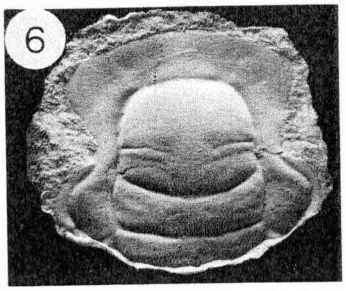
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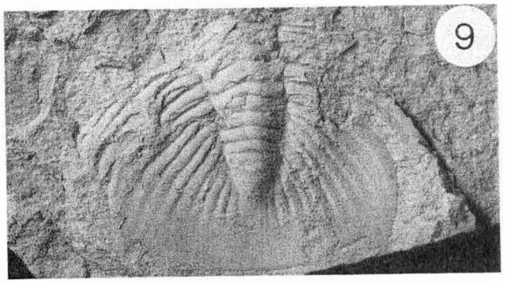
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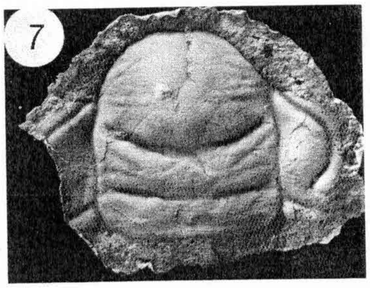
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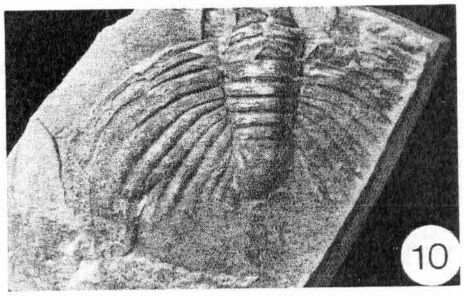
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Plate 5

Fig. 1. GSC75189. Cranidium. Mistaya Formation, southern Alberta. Site 260.2 of Westrop, 1986a. x 1.

Fig. 2. GSC75189. Posterior view of cranidium illustrated above, showing upstanding palpebral lobe. x 1.

Fig. 3. GSC75189. Olique lateral view of palpebral lobe illustrated above. x 1.

Fig. 4 & 5. UW4006-224. Free cheek. Laminated sandstone. West of Wilton, Monroe County, Wisconsin. x 1.

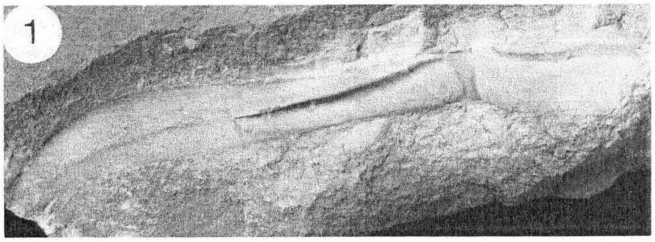
Fig. 6. FMNH. PE39205. Latex cast of external mold of cranidium showing intercalated furrows. Chippewa River Falls (CR). x 1.

Fig. 7. LACMIP29242. Latex cast of external mold of cranidium showing intercalated furrows. Locality unknown. x 1.

Fig. 8. UW4006-434. Yoked free cheek with hypostome attached. North Freedom Bed 8 (NF). x 0.75.

Fig. 9. UW4006-196a. Pygidium with articulated thoracic segments. North Freedom Bed 2 (NF). x 1.

Fig. 10. UW4006-130. Pygidium with articulated thoracic segments. North Freedom Bed 8 (NF). x 0.5.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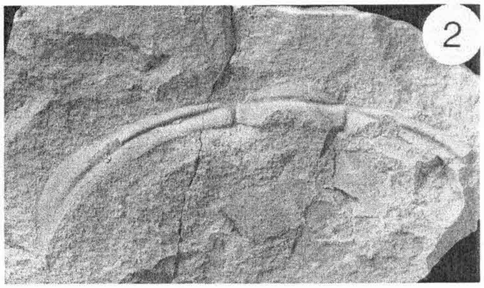
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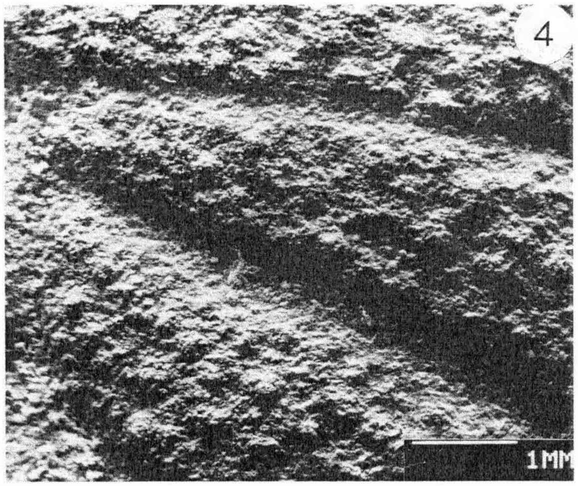
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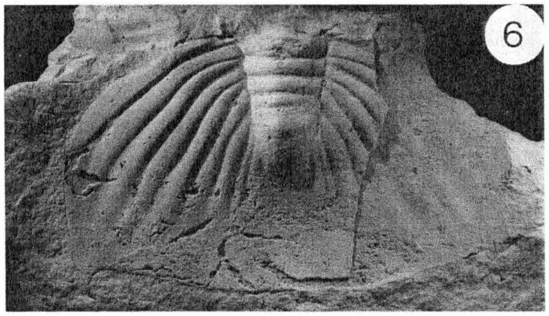
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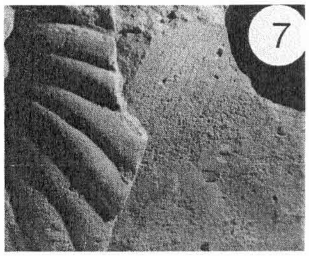
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Plate 6

Fig. 1. UW4006-441. Segment from anterior part of thorax. North Freedom Bed 2 (NF). x 1.

Fig. 2. UW4006-424. Segment from posterior part of thorax. North Freedom Bed 2 (NF). x 1.

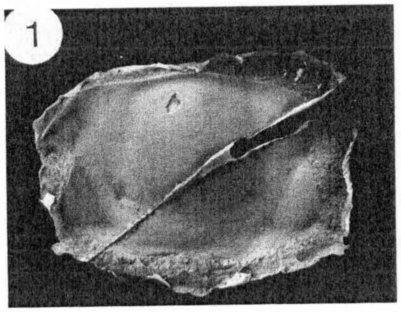
Fig. 3. UMPC-R2443nn. Latex cast of an incomplete pygidium showing fine pustulation on pleurae. Hokah (HH). x 1.

Fig. 4. USNM443597. SEM of latex cast of pustules on pleural plaftorm of pygidium. Mauston Quadrangle. (MN).

Fig. 5. SMM34-2091A. Free cheek showing terracing on doublure. Fariy Glen (SWa). x 1.

Fig. 6. AMNH39094. Pygidium. Figured by Hall (1863, pl. 9, fig. 7) Laminated sandstone. Madison (MS). x 0.5.

Fig. 7. AMNH39094. Detail of pygidium figured above showing extent of doublure. x 1.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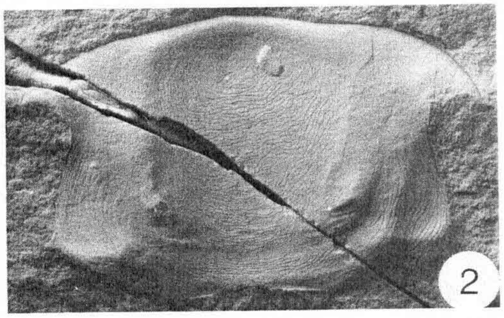
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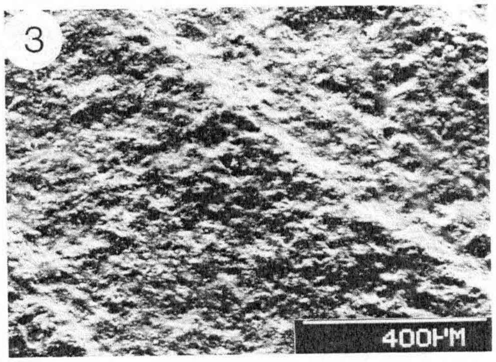
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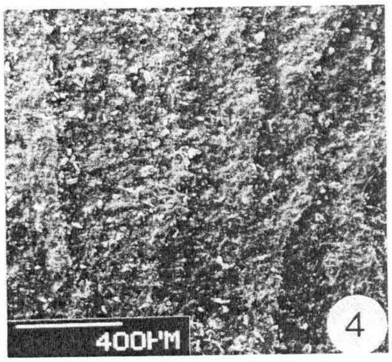
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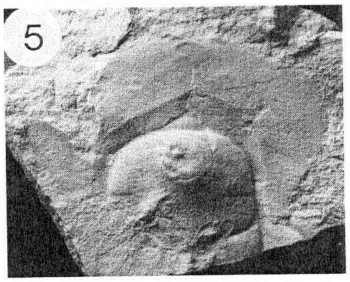
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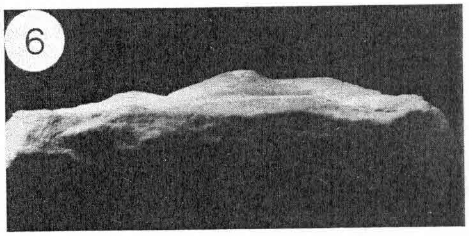
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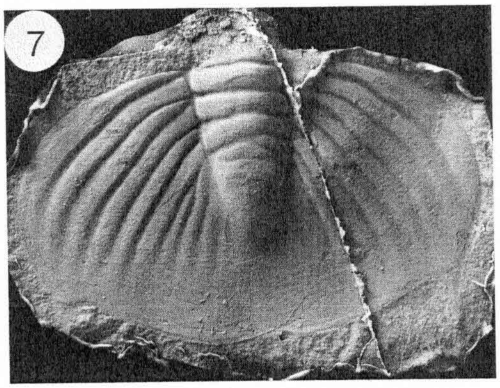
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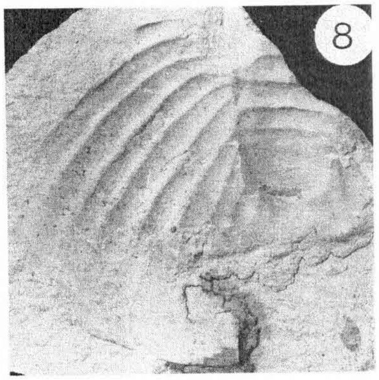
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Plate 7

Fig. 1. UW4006-276. Latex cast of eternal mold of hypostome showing strong terrace ridges. Aracdia (AAa). x 1.

Fig. 2. UW4006-276. External mold of hypostome figured above. x 1.5.

Fig. 3. UW4006-276. SEM of latex of cuesta-like terraces on posterior margin of hypostome figured above.

Fig. 4. UW4006-276. SEM of latex of upstanding terraces on median body of hypostome figured above.

Fig. 5. UW4006-70. Cranidium showing bulbous feature on anterior lobe. North Freedom Bed 2 (NF). x 1.

Fig. 6. UW4006-70. Anterior view of cranidium figured above. North Freedom Bed 2 (NF). x 1.

Fig. 7. USNM443598. Latex cast of external mold of pygidium showing axial and pleural abnormality. Locality unknown. x 1.

Fig. 8. UW4006-81. Counterpart of pygidium showing arcuate embayment in lateral margin. North Freedom Bed 2 (NF). x 0.75.