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Résumé de l'article

Des spécimens de l'ichnospece *Rusophycus* et *Cruziana* conservés sur une plaquette recueillie d'un talus de la Formation de l'Ordovicien moyen tardif de Lotbinière découverte aux chutes Montmorency, au nord-est de Québec, sont représentés et décrits. On limitait les trilobites benthiques ultérieurs à l'Ordovicien, présumés producteurs de ces ichnotaxons dans les scénarios marins, à des niches écologiques généralement en eau peu profonde. Les taxons de trilobites plus anciens habitaient un vaste éventail d'environnements, comme l'a également révélé la présence de ces ichnotaxons dans la Formation de Lotbinière. Leur présence dans cette Formation, qui constitue indubitablement une séquence de microfisch sédimentaire, laisse supposer qu'il faudrait se montrer prudent, quand elles apparaissent de façon isolée, vis-à-vis de l'importance paléoenvironnementale de ces ichnotaxons, particulièrement dans les strates de la période du Cambrien et de l'Ordovicien. L'orientation ordonnée et interprétée comme plutôt rhéotique du *Rusophycus* permet de supposer l'existence de courants de fond pendant la production des traces.

[Traduit par la rédaction]

Deep-water marine *Rusophycus* and *Cruziana* from the Ordovician Lotbinière Formation of Quebec

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Specimens of *Rusophycus* isp. and *Cruziana* isp. preserved on a slab collected from talus of the late Middle Ordovician Lotbinière Formation exposed at Montmorency Falls, northeast of Quebec City, are figured and described. Post-Ordovician benthic trilobites, in marine scenarios the presumed producers of such ichnotaxa, were restricted to generally shallow-water ecological niches. Older trilobite taxa inhabited a wide spectrum of environments, as also reflected in the occurrence of these ichnotaxa in the Lotbinière Formation. Occurrence of these ichnotaxa in the Lotbinière Formation, an undoubted basinal microflysch sequence, suggests that caution should be exercised, when occurring in isolation, with respect to the palaeoenvironmental significance of these ichnotaxa, particularly in strata of Cambrian and Ordovician age. A non-random and, instead, an interpreted rheotactic orientation of *Rusophycus* suggests the existence of bottom currents during production of the traces.

Des spécimens de l'ichnoespèce *Rusophycus* et *Cruziana* conservés sur une plaquette recueillie d'un talus de la Formation de l'Ordovicien moyen tardif de Lotbinière découverte aux chutes Montmorency, au nord-est de Québec, sont représentés et décrits. On limitait les trilobites benthiques ultérieurs à l'Ordovicien, présumés producteurs de ces ichnotaxons dans les scénarios marins, à des niches écologiques généralement en eau peu profonde. Les taxons de trilobites plus anciens habitaient un vaste éventail d'environnements, comme l'a également révélé la présence de ces ichnotaxons dans la Formation de Lotbinière. Leur présence dans cette Formation, qui constitue indubitablement une séquence de microflysch sédimentaire, laisse supposer qu'il faudrait se montrer prudent, quand elles apparaissent de façon isolée, vis-à-vis de l'importance paléoenvironnementale de ces ichnotaxons, particulièrement dans les strates de la période du Cambrien et de l'Ordovicien. L'orientation ordonnée et interprétée comme plutôt rhéotatique du *Rusophycus* permet de supposer l'existence de courants de fond pendant la production des traces.

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INTRODUCTION

Trace fossils have proven to be powerful tools in a variety of sedimentological, palaeontological and palaeoenvironmental studies of different aspects (Ekdale *et al.*, 1984). Regrettably, however, many palaeontologists continue to consider certain individual ichnotaxa as indicative of specific palaeoenvironments. For example, in post-Early Cambrian strata (see Crimes and Anderson, 1985), the ichnogenus *Paleodictyon* Meneghini in Murchison, 1850 is still almost universally regarded as a definitive indicator of deep-marine basinal palaeoenvironments, yet it has recently been recorded from shelf (Paczeńska, 1985; Stanley and Pickerill, 1993a; Pek *et al.*, 1994), marginal marine (Archer and Maples, 1984) and even nonmarine (Pickerill, 1990) environments. The ichnogenera *Rusophycus* Hall, 1852 and *Cruziana* d'Orbigny, 1842, the subjects of this contribution, are no exception to this generalization. Traditionally, in marine situations these ichnotaxa have invariably been documented from, and reported as indicators of, shallow nearshore and shelf deposits and, indeed, in Palaeozoic strata they are generally still considered as specific representatives of the shallow-water marine *Cruziana* ichnofacies of Seilacher (1967). This short paper demonstrates that, as with *Paleodictyon*, there are generally

exceptions to the rule and that caution should be exercised in the utilization of discrete ichnotaxa as definitive palaeoenvironmental indicators.

The purpose of this contribution is, therefore, to document an apparently palaeoenvironmentally anomalous occurrence of the ichnogenera *Cruziana* and *Rusophycus*, namely from deep-water marine strata of the Lotbinière Formation (Ordovician) of Quebec, eastern Canada. Although previous recordings of deep-water *Rusophycus* and *Cruziana* have been made (Pickerill *et al.*, 1988) these were based on generally poorly preserved and isolated specimens. Perhaps more important, however, is the fact that most subsequent authors have ignored or are unaware of such isolated recordings and therefore still utilize these ichnotaxa as definitive palaeoenvironmental indicators. The material described herein is more abundant than previously described deep-water examples and its palaeoenvironmental occurrence is unequivocal.

LOCATION AND GEOLOGIC BACKGROUND

Specimens of *Rusophycus* and *Cruziana* reported herein are preserved on the sole of a thin, (5 mm or less), parallel laminated siltstone slab collected from locally derived talus of

the Lotbinière Formation at Montmorency Falls, located approximately 10 km northeast of the city of Québec along the north shore of the St. Lawrence River, eastern Canada (Fig. 1). The Lotbinière Formation, originally defined by Clark and Globensky (1975), comprises a sequence of graptolitic, micaceous silty shales (>90%) with regularly developed and generally undisturbed (non-bioturbated) siltstone laminae, and rare (<10%) and thin (generally less than 2 cm) fine-grained sandstone interbeds (Belt *et al.*, 1979). At Montmorency Falls, more than 200 m of the formation are exposed (see Belt *et al.*, 1979, fig. 3; Riva and Pickerill, 1987, fig. 5) and graptolites preserved in the sequence are indicative of the *Climacograptus spiniferus* Zone (late Middle Ordovician). Belt *et al.* (1979) have discussed the depositional environment of the Lotbinière Formation in detail, concluding that it represents a distal microflysch deposited in deep basinal conditions that existed between or beyond coeval submarine fan systems. The present author agrees with this interpretation, though of course absolute depth *per se* is impossible to realistically assess.

SYSTEMATIC ICNOLOGY

Material

The collected slab, approximately 25 x 20 cm (Fig. 2A), contains a minimum of 25 examples of *Rusophycus* and 5 of *Cruziana*. Segments of additional specimens also occur, but because of overlap, poor preservation or truncation at the edge of the slab, are not confidently identifiable. The slab is housed in the Division of Natural Sciences, New Brunswick Museum, Saint John, New Brunswick with repository number NBMG 9946.

Description

Because of the generally poor preservation of the material, ichnospecific assignment is unwarranted and, therefore, the two ichnotaxa are briefly described at the ichnogenetic rank only. More recent diagnoses of the ichnogenera and their nomenclatural history are given in Fillion and Pickerill (1990) and Keighley and Pickerill (1995).

Ichnogenus Rusophycus Hall, 1852 (Fig. 2)

Specimens of *Rusophycus*, preserved in presumed convex hyporelief, comprise relatively shallowly impressed and variably preserved bilobed structures that range in size from a maximum of 30 mm (length) by 20 mm (width) to 16 mm by 9 mm. Lobes are parallel or merge slightly posteriorly; they possess variably developed but generally poorly preserved and delicate unid scratch markings that are transverse or are slightly directed antero-laterally. In better preserved examples the scratch markings generally extend to the lateral margins of the specimens. The lateral margins themselves are relatively sharp and steep. Median furrows are variably preserved but appear to be generally undisturbed. Coxal, exopodal, spinal, cephalic and pygidial markings are absent.

Ichnogenus Cruziana d'Orbigny, 1842 (Fig. 2)

Specimens of *Cruziana* are very poorly preserved, but each comprises a generally bilobed and elongate, shallowly impressed repichnion preserved, like *Rusophycus*, in presumed convex hyporelief. Specimens range in size from a maximum of 53 mm (length) by 14 mm (width) to a minimum of 34 mm by 13 mm. Lobes and median furrows are poorly developed; their lobate configuration is best developed at the generally sharp and steep external margins where, in addition, faint, transversely oriented, unid scratch markings are typically present. Median structures are not preserved.

Remarks

Despite the generally poor preservation of this material, in part presumably a result of intense compaction, it can be confidently assigned to the ichnogenera *Rusophycus* and *Cruziana*. Like in most recent articles, in this contribution the distinction between *Cruziana*, representing the repichnia (locomotory activity), and *Rusophycus* as the cubichnia (resting activity) of arthropods, in marine environments presumably trilobites (Seilacher, 1970, 1985), is retained (*contra* Seilacher, 1970). While recognizing that on rare occasions the distinction between the two is problematical, in most situations they are easily distinguishable. Additionally, of course, and perhaps more importantly, each represents a fundamentally different behavioural pattern, an important consideration with respect to nomenclatural taxonomic procedures (Bromley, 1990). All specimens of *Rusophycus* as identified herein possess a shape factor (length:width ratio - see Crimes, 1970) of between 1.1 (minimum) and 2.0 (maximum), with a mean of 1.6, consistent with the limits of the ichnotaxon as recently discussed by Keighley and Pickerill (1996). The few (5) examples of *Cruziana* each exhibit a shape factor of >2.0 (maximum 3.7, mean 2.9), reflecting forward movement of the producing organisms. Although the two ichnogenera exhibit markedly different shape factors, it is notable that there is no obvious separation with respect to their respective widths, possibly suggesting that both were produced by a single population of conspecific arthropods (cf. Brandt, 1995).

As easily discerned in Figure 2A, with the exception of two specimens, 23 examples of *Rusophycus* exhibit a preferred orientation with respect to their median long axes. Indeed, measurements of these long axes indicate that they diverge by only 38°, with the majority (65%) being aligned within 10° or so of each other. It is tempting to equate this obviously preferred orientation, and indeed is interpreted herein, as resulting from rheotrophism (rheotaxis) (cf. Crimes *et al.*, 1977). If this is the case, then it would suggest that these examples of *Rusophycus* were formed at the sediment-water interface in response to a bottom-current perhaps as a function of feeding, respiration, protection, or some other biological consideration. Irrespective of the underlying reason(s) for the preferred alignment, such an orientation does suggest formation of the structures surficially. This is important with respect to the ongoing debate on the production of both *Rusophycus* and *Cruziana*

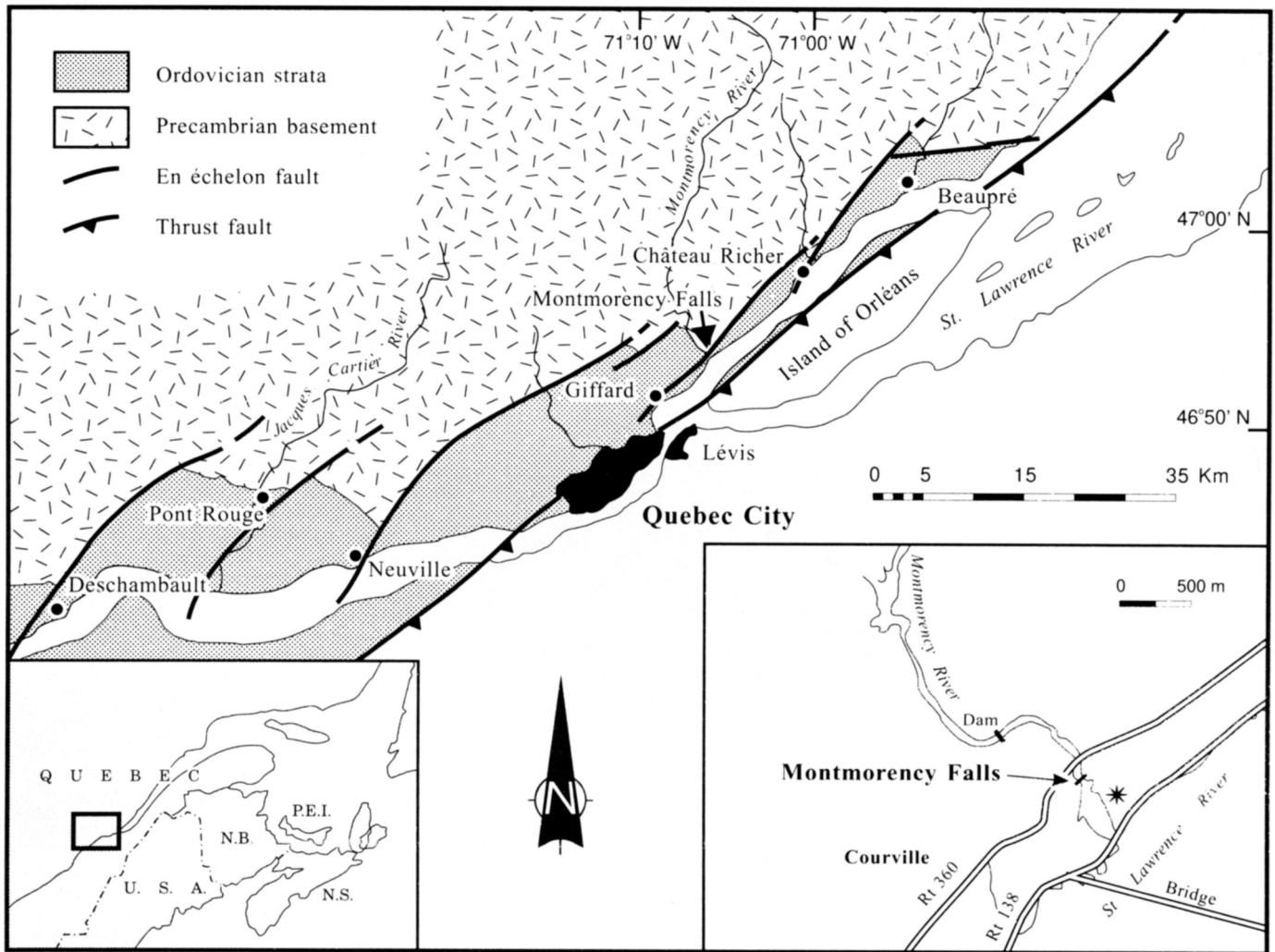


Fig. 1. Simplified geology of the Quebec City area and detailed location of Montmorency Falls and trace-fossil location (asterisk) of material described herein.

as either surficial (cf. Baldwin, 1977) or infaunal (cf. Goldring, 1985) in origin. Clearly, at least in this case, a surficial origin can be inferred for the production of the structures described herein and, therefore, despite the convincing arguments of an infaunal origin presented by Goldring (1985) on the formation of such ichnotaxa, the origin of such structures should remain equivocal and each occurrence should be assessed individually. Of interest are the two examples of *Rusophycus* that do not show the obvious preferred orientation exhibited by the remainder (open-arrowed in Fig. 2A). These two examples are less deeply impressed and clearly pre-date the aligned specimens, as indicated by cross-cutting relationships, suggesting earlier formation and an orientation not necessarily in response to any prevailing bottom-current.

DISCUSSION

Undoubtedly, as previously noted, the vast majority of *Rusophycus* and *Cruziana* documented from marine strata are from shallow-shelf sequences. Indeed, characteristically, these two arthropod-produced (in marine environments most likely trilobites - see Osgood, 1970; Seilacher, 1970, 1985)

ichnogenera are integral components and specific indicators of the shallow-marine *Cruziana* ichnofacies of Seilacher (1967). Yet in ichnological studies it is becoming increasingly recognized that caution must be exercised in the utilization of discrete ichnotaxa as reliable and unequivocal palaeoenvironmental indicators. For example, Bottjer *et al.* (1988) and Bottjer and Droser (1994) have provided convincing evidence of the progressive movement to offshore and deeper-water environments of the ichnotaxon *Zoophycos* Massalongo, 1855 following the Palaeozoic; Crimes and Crossley (1991) and Crimes *et al.* (1992) have suggested that *Paleodictyon* 'evolved' in Early Cambrian shallow-water niches and then 'retreated' to deeper-water habitats; Stanley and Pickerill (1993b) have noted that all documented Palaeozoic examples of *Fustiglyphus* Vialov, 1971 are from nearshore or shelf sequences, while those of Mesozoic and Cenozoic age are from deep-water flysch successions, and Han and Pickerill (1994) observed that pre-Carboniferous occurrences of *Protovirgularia* M'Coy, 1850 were from deep-water sequences whereas post-Carboniferous examples were from nearshore and shelf environments. Detailed studies on selected and stratigraphically long-ranging ichnogenera such as these

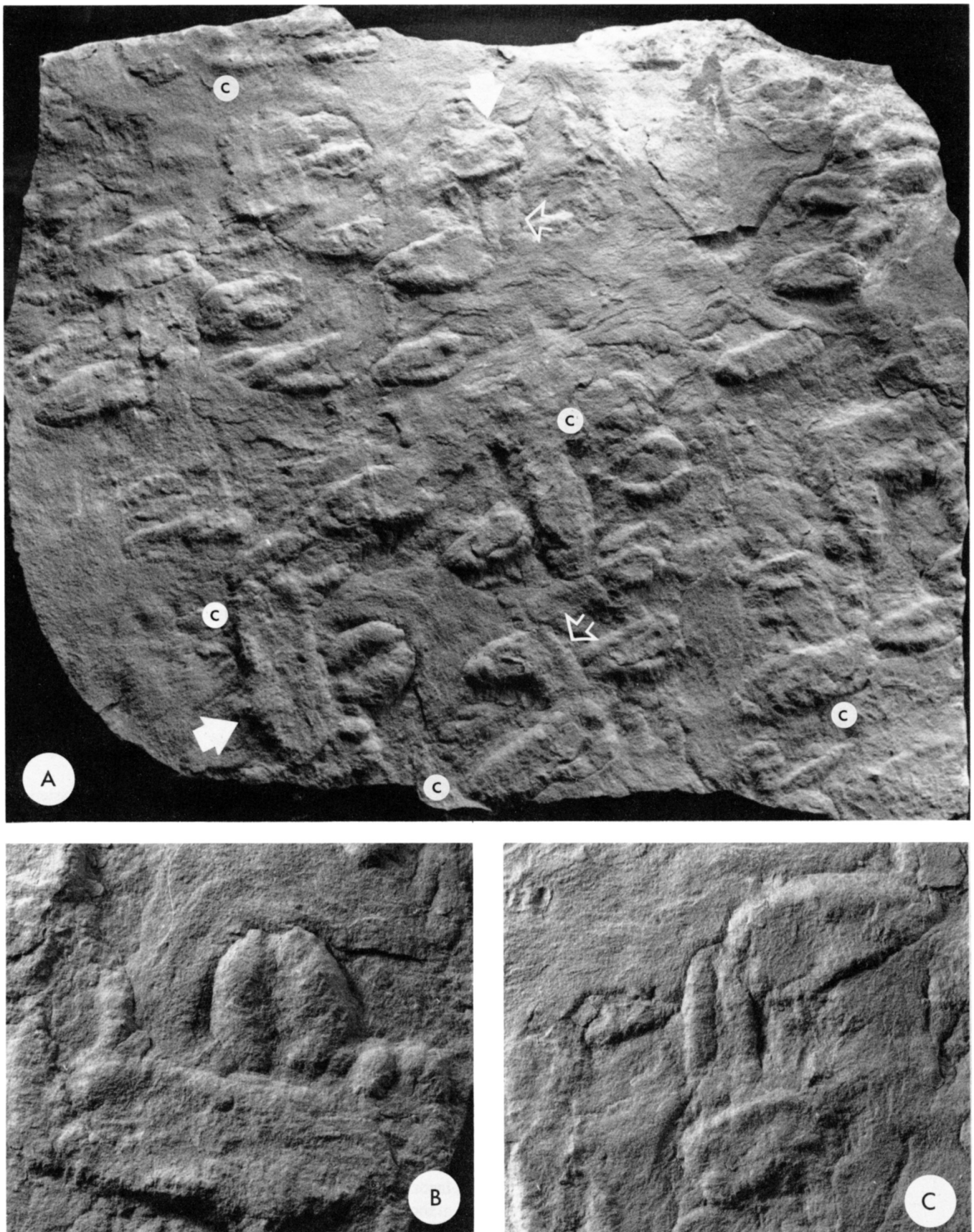


Fig. 2. (A) Slab preserving *Rusophycus* isp. and *Cruziana* isp. (labeled c) as described herein from the Ordovician Lotbinière Formation of Quebec, NBMG 9946. Lower solid arrow represents orientation of Figure 2B and upper solid arrow of Figure 2C. The two open arrows indicate examples of *Rusophycus* not showing a preferred orientation (see text for details); x0.73. (B, C) Enlargements of *Rusophycus* indicated by solid arrowed areas as shown in (A); (B) is area indicated by lower solid arrow and (C) of upper solid arrow; note that in both examples cross-cutting relationships indicate an earlier formation for both specimens; x1.5. Note poorly preserved scratch markings on each specimen.

are important in that they do illustrate that the palaeoenvironmental preferences of the producers of certain individual ichnotaxa, and for various reasons, may well have changed over time. Undoubtedly, therefore, if one ignores the obviously facies-independent, stratigraphically long-ranging and commonly recorded ichnotaxa such as *Chondrites* von Sternberg, 1833, or the variety of short-lived specialized forms such as those recently reviewed by Crimes (1994), or those trace fossils, commonly monoichnospecific, recorded from isolated occurrences (see Pemberton and Frey, 1982; Norman and Pickerill, 1995), then it is important to document apparently anomalous recordings of additional ichnotaxa in order to assess possible evolutionary trends in palaeoenvironmental occurrence.

That the palaeoenvironment of the Lotbinière Formation is deep-water basinal marine is uncontested. The sequence at Montmorency Falls, regarded as a reference section for the formation (Riva and Pickerill, 1987), has been discussed in detail by Belt *et al.* (1979) who regarded it a basinal microflysch deposited as a result of the downwarping or collapse of the outer margins of the Laurentian Platform caused by the approach of the Taconic allochthons from the southeast. The Lotbinière Formation itself was derived from erosion of the Taconic masses that were finally emplaced at the end of Middle Ordovician time when prodeltaic sediments gradually filled the then shallowing basin that had formed northwest of the newly-emplaced Taconic Mountains (Riva and Pickerill, 1987, and references therein). Thus, there is little doubt that the examples of *Cruziana* and, particularly, *Rusophycus*, recorded herein occur in deep-water strata.

What then of the possible significance of the recordings documented herein? Regrettably, there are too few reports of deep-water marine *Cruziana* and *Rusophycus* to advance any potential palaeoenvironmental trends in their distribution over time. To this author's knowledge, one or both ichnotaxa have only commonly been recorded in deep-water strata from the Cambrian of Nova Scotia (Pickerill, 1992; Pickerill and Waldron, 1992 - *Rusophycus*) and the Ordovician of New Brunswick (Pickerill *et al.*, 1988 - *Cruziana* and *Rusophycus*). Importantly, however, all such recordings are from strata of Cambrian or Ordovician age; no significant post-Ordovician occurrences have, to date, been documented. Despite the lack of additional recordings in deep-water strata of Cambrian-Ordovician age, it is notable that in the Late Ordovician, trilobites, the presumed progenitors, became less abundant, both in terms of species and individuals, and it was a time of major restructuring of shelf and basinal invertebrate communities (Boucot, 1983). In contrast to Cambrian-Ordovician trilobites, adapted to a wide spectrum of environments, Silurian and younger representatives of all trilobite families were restricted to generally shallow-water ecological niches (see Thomas and Lane, 1984; Robison and Kaesler, 1987). If one assumes that trilobites were the producers of marine *Cruziana* and *Rusophycus*, then it is therefore hardly surprising that relatively few deep-water post-Ordovician examples have been recorded (e.g., Han and Pickerill, 1994) and that in post-Ordovician to Triassic strata these ichnotaxa can generally still be regarded as useful shallow-water palaeoenvironmental indicators. Nevertheless, as reflected in the known

palaeoecological distribution of earlier trilobites and indeed evidence of their behavioural activity, as for example documented herein, caution must be exercised in their utilization as palaeoenvironmental indicators in strata of Cambrian and Ordovician age. Undoubtedly, even in rocks of this age the majority of examples are present in shallow-marine sequences. Yet exceptions do occur and predictably additional deep-water recordings of these ichnotaxa will be made in strata of this age, paralleling what is known of trilobite palaeoecology in general.

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