Shallow marine *Paleodictyon* from the Upper Ordovician Georgian Bay Formation of southern Ontario

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Two specimens, and a possible third, of the ichnotaxon *Paleodictyon* are documented from shallow-water marine strata of the Upper Ordovician Georgian Bay Formation of southern Ontario. Its occurrence indicates that previous suggestions of a post-Early Cambrian palaeoenvironmental retreat of *Paleodictyon* into deeper water require some modification. Instead, the operative migratory process, at least to the Late Ordovician and possibly even longer, was one of expansion and not of retreat.

Deux spécimens, et possiblement un troisième, de la trace fossile *Paléodictyon* sont reconnus dans des strates marines peu profondes de la Formation de Georgian Bay de l'Ordovicien supérieur du sud de l'Ontario. Sa présence indique que les suggestions précédentes d'une retraite paléo-environnementale post-Cambrien précoce de *Paléodictyon* en eaux plus profondes nécessitent quelques modifications. À la place, le processus migratoire opératif, au moins jusqu'à l'Ordovicien tardif et possiblement encore plus longtemps, en était un d'expansion et non de retraite.

[Traduit par la rédaction]

Introduction

Several recent studies in ichnology have demonstrated or suggested an environmental shift in the distribution of certain marine ichnotaxa throughout their known stratigraphic range. For example, Bottjer *et al.* (1988) demonstrated that the ichnogenus *Zoophycos* Massalongo, while common in both shelf and deep-sea environments in the Palaeozoic, has only been reported from deep-sea successions in post-Palaeozoic strata. These authors also showed that *Ophiomorpha* Lundgren, that supposedly first appeared in Permian shallow-water environments and was common in deep-sea environments by the Cretaceous, has been distributed from nearshore to deep-sea environments since then. Similarly, Stanley and Pickerill (in press) suggested that the ichnotaxa *Fustiglyphus* Vialov and *Rhabdoglyphus* Vassoievich occupied only shallow-water regimes in the Palaeozoic and deep-water regimes in the Mesozoic and Tertiary. Bottjer *et al.* (1988) termed the migration of marine ichnotaxa offshore into deep-water regimes but with persistence of representatives onshore as 'expansion', and movement offshore into deep-water regimes but with loss of onshore representatives as 'retreat'.

In recent contributions by Crimes and Crossley (1991) and Crimes *et al.* (1992) it was suggested that the ichnotaxon *Paleodictyon* Meneghini, the subject of this short paper, 'evolved' in shallow-water Early Cambrian regimes. These authors suggested that, with two exceptions of records of non-marine occurrences by Archer and Maples (1984) and Pickerill (1990), the ichnotaxon became restricted to deep-water marine environments in post-Early Cambrian regimes. In this contribution, not only do we record and describe the first examples of *Paleodictyon* from any sequence in Ontario, but also we demonstrate that its occurrence there suggests that the environmental 'retreat' intimated by Crimes and Crossley (1991) and Crimes *et al.* (1992) is not so straightforward as they suggested.

Location, Stratigraphic and Palaeoenvironmental Setting

Specimens discussed herein are from three locations within the Upper Ordovician (upper Maysvillian-lower Richmondian) Georgian Bay Formation of southern Ontario (Fig. 1). A single specimen was present at each of the locations and these are housed in the Royal Ontario Museum. The locations, with appropriate ROM catalogue numbers for each specimen, are:-

(1) The Humber River Valley (Baby Point), Toronto. N.T.S. co-ordinates 4834250 m N x 620750 m E (ROM 49424).
(2) Workman's Creek, southeast of Meaford. N.T.S. co-ordinates 4938000 m N x 534800 m E (ROM 49624).
(3) Highway 401 at Highway 403 overpass, Mississauga. N.T.S. co-ordinates 4832500 m N x 620750 m E (ROM 49625).

The Georgian Bay Formation is an essentially siliciclastic sequence of interbedded calcareous sandstones and grey, grey-blue or green bioturbated mudstones that is about 177 m thick in the Toronto area and thins northward to approximately 127 m thick in the Georgian Bay area. The formation can be broadly categorized as upward-coarsening and upward-thickening. Mudstone with thinly-layered sandstones are predominant in its lower horizons whereas generally thicker-bedded and sandstone-dominated sequences with sub-

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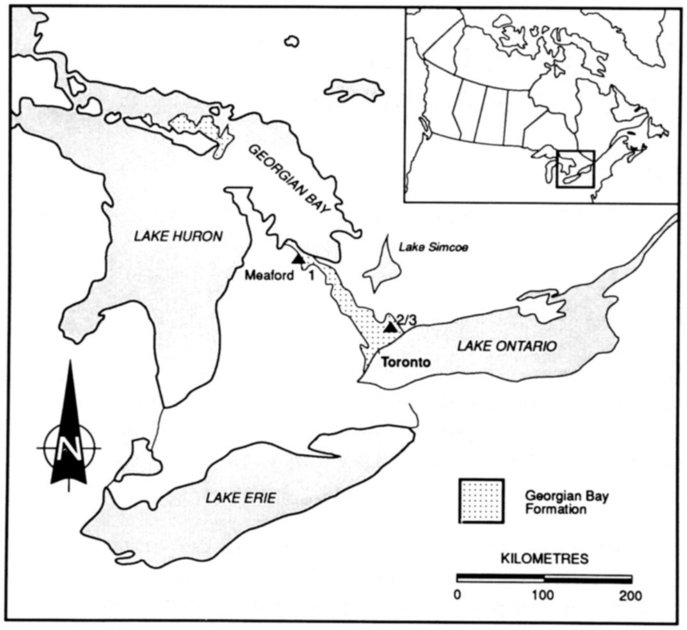


Fig. 1. Surficial distribution of the Georgian Bay Formation of southern Ontario. 1 = Workman's Creek, southeast of Meaford; 2/3 = Humber River Valley/Highway 401 localities (see text for details).

ordinate mudstones comprise the upper horizons. The relative proportions of mudstone-dominated and sandstone-dominated sequences varies according to present-day location. The formation forms the middle part of an upward-shallowing, progradational sequence from the relatively deep-water mudstones of the underlying Blue Mountain Formation to the muddy, tidal-flat sequences of the overlying Queenston Formation (Russell and Telford, 1983; Middleton, 1987).

Kerr and Eyles (1991) have recently discussed the depositional history of the Georgian Bay Formation in some detail. These authors concluded that the sequence was deposited on a storm-influenced mid- to outer-shelf originally located in equatorial palaeolatitudes. Sedimentological observations suggested that most of the sequence was deposited between fair-weather and storm-wave base. We generally concur with this conclusion, that is also corroborated by the occurrence within the succession of trace fossils characteristic of both the shallow marine *Skolithos* and *Cruziana* ichnofacies of Seilacher (1964, 1967). In additon to *Paleodictyon* these ichnotaxa include: *Arthraria antiquata*, *Aulichnites parkerensis*, *Chondrites* isp., *Cochlichnus anguineus*, *Cochlichnus* isp. nov., *Cruziana lobosa*, *Cruziana problematica*, *Cruziana quadrata*, *Cruziana* isp., *Curvolithus multiplex*, *Didymaulichnus lyelli*, *Diplocraterion* cf. *biclavatum*, *Diplocraterion helmerseni*, *Diplocraterion parallelum*, *Fustiglyphus annulatus*, *Gordia marina*, *Gyrochorte comosa*, *Helminthopsis hieroglyphica*, *Lingulichnus verticalis*, *Lockeia siliquaria*, *Micatuba verso*, *Monocraterion* isp., *Monomorphichnus bilinearis*, *Monomorphicnus lineatus*, *Palaeophycus annulatus*, *Palaeophycus heberti*, *Palaeophycus striatus*, *Palaeophycus tubularis*, *Phycodes flabellus*, *Phycodes palmatus*, *Planolites beverleyensis*, *Planolites* isp. nov., *Rusophycus carbonarius*, *Rusophycus polonicus*, *Rusophycus cryptolithi*, *Rusophycus pudicus*, *Skolithos magnus*, *Skolithos verticalis*, *Trichophycus lanosus*, *Trichophycus venosus* and *Walcottia rugosa*.

SYSTEMATIC PALICHNOLOGY

Ichnogenus *Paleodictyon* Meneghini in Murchison, 1850

Type ichnospecies: *Paleodictyon strozzii* Meneghini, 1850 by monotypy.

Diagnosis: Honeycomb-like network of four- to eight-sided, usually hexagonal, horizontal meshes, preserved typically in convex hyporelief, more rarely in concave epirelief. Meshes with or without vertical outlets, of variable size and shape. Outline of entire systems rounded, or more typically hexagonal (after Pickerill, 1990).

Paleodictyon isp. A
Figure 2A, B

Material: Two specimens: ROM 49424 and ROM 49624.

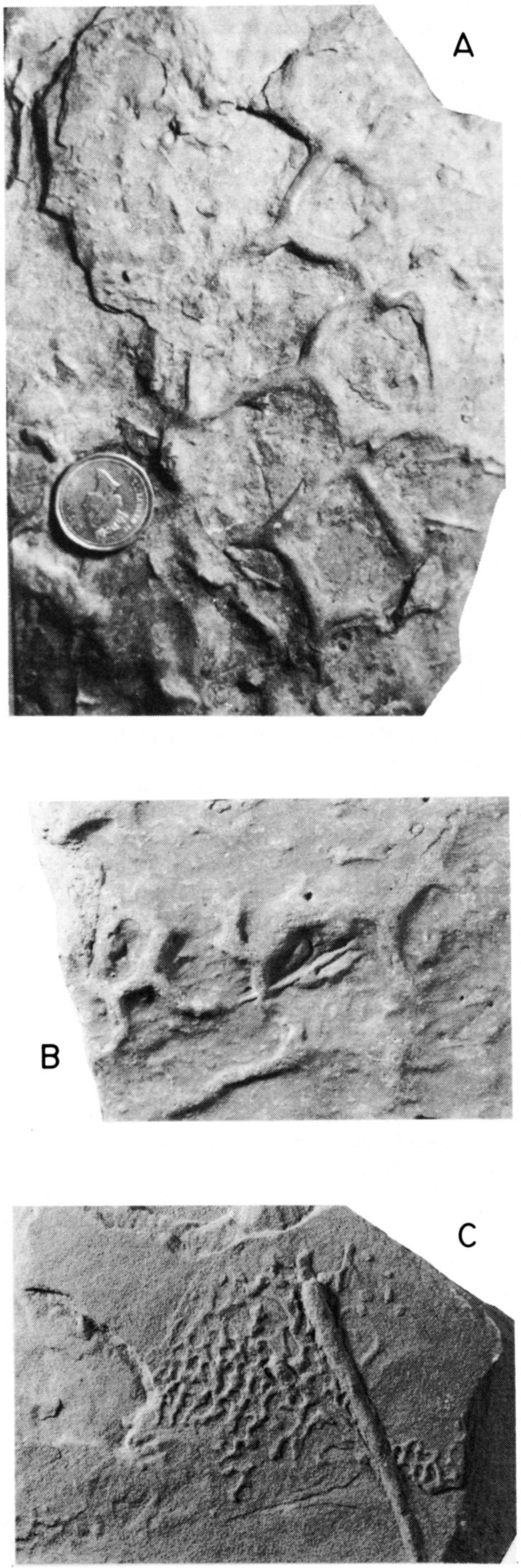
Description: Specimens preserved as smooth convex hyporeliefs on the soles of 2 cm-thick, fine-grained, hummocky cross-stratified, grey calcareous sandstone layers. Both specimens consist of moderately- to well-preserved, incomplete, horizontal, irregularly polygonal meshes defined by curved to straight smooth riblets 4 to 5 mm in diameter, up to 3 mm in height, bearing elliptical cross-sections. Individual polygons, where preserved, range in size, from 1.8 to 2.9 cm diagonally. The two specimens cover surface areas of 24 to 56 cm^2.

?*Paleodictyon* isp. B
Figure 2C

Material: One specimen: ROM 49625.

Description: Specimen comprises an 11 cm^2, relatively complete, moderately well-preserved, though poorly-defined, horizontal mesh preserved in convex hyporelief on the sole of a 2.5 cm thick, fine-grained calcareous sandstone. Smooth, straight to curved riblets, 1 to 2 mm wide by 0.5 mm high, define irregular polygons ranging in size from 1 to 2 mm across.

Remarks: As noted by McCann and Pickerill (1988) and discussed in more detail by Crimes and Crossley (1991), ichnospecific classification of the many forms of *Paleodictyon* is muddled and the ichnotaxon is in need of taxonomic revision. We therefore designate our material only at the ichnogeneric rank. We do note, however, that in terms of size and overall net arrangement, *Paleodictyon* isp. A compares reasonably closely with both *P.* (*Glenodictyum*) *imperfectum* Seilacher and *P. giganteum* Peruzzi, both of which are



exceptionally large forms. ?*Paleodictyon* isp. B is only tentatively identified as such because we cannot confidently ascertain well-developed polygons characteristic of the ichnotaxon. Additionally, superficially similar examples have been described by authors such as Osgood (1970) and Benton and Gray (1981) as being inorganic in origin.

DISCUSSION

The ichnotaxon *Paleodictyon* has previously been recorded in eastern Canada from the Cambrian of Newfoundland (Crimes and Anderson, 1985) and Nova Scotia (Pickerill and Keppie, 1981; Waldron, 1988), and the Carboniferous of New Brunswick (Pickerill, 1990). To our knowledge, this is its first recording from Ontario and, indeed, its first documented occurrence in Canada in rocks of Ordovician age. As briefly reviewed by Pickerill (1990) and Crimes and Crossley (1991), the origin and function of *Paleodictyon* have been actively debated since its initial description by Meneghini (*in* Murchison, 1850). Although most researchers now accept a biogenic origin, several enigmas still remain to be resolved (see also Miller, 1991). Unfortunately, the small amount of material from the Georgian Bay Formation and its generally poor and incomplete preservation precludes consideration of these enigmas. Nevertheless, its occurrence there in an Ordovician shelf setting, as interpreted for the formation, is worthy of additional commentary.

As noted previously, several authors (e.g., Crimes and Crossley, 1991; Crimes *et al.*, 1992) have suggested that *Paleodictyon* initially 'evolved' in Early Cambrian shallow water niches and then 'retreated' to deeper-water habitats. Bottjer and Jablonski (1988) and Crimes and Droser (1992) suggested that the process of environmental 'retreat' was biologically-driven and that possible mechanisms included competitive exclusion by superior innovations that originated onshore and, or, passive replacement, because speciation in more stable offshore environments may have been more predictable than in less stable onshore equivalents. Whatever the cause, with respect to *Paleodictyon* the environmental 'retreat' intimated by Crimes and Crossley (1991) and Crimes *et al.* (1992) is obviously not so straightforward as suggested. Initially, it must be recalled that Archer and Maples (1984) and Pickerill (1990) recorded *Paleodictyon* in non-marine strata of Carboniferous age. This suggests that the 'retreat' process also involved non-marine as well as offshore or deep-sea habitats. Retreat into non-marine habitats is not included within the definitions of 'retreat' and 'expansion' by Bottjer *et al.* (1988). Instead, the descriptor 'amphidromy' has been utilized by Maples and Archer (1989) to reflect the migration of marine ichnotaxa into a non-

Fig. 2. (A) *Paleodictyon* isp. A from the Humber River Valley (Baby Point), Toronto (ROM 49424), x 0.8; (B) *Paleodictyon* isp. A from Workman's Creek (ROM 49624), x 0.6; (C) ?*Paleodictyon* isp. B from Highway 401 at Highway 403 overpass, Mississauga (ROM 49625), x 0.8. All specimens preserved in positive hyporelief.

marine environment (or vice versa). Implicit in the concept of amphidromy is that it may or may not involve retreat or expansion, though predictably expansion would be the norm. Providing a non-marine ichnotaxon does not simply reflect behavioural convergence, that is difficult if not impossible to demonstrate, then it is logical to assume that any amphidromic process is initiated from shallow-water marine environments. Indeed, amphidromy is prevalent today among organisms in nearshore environments and undoubtedly was well-established in the Palaeozoic (Maples and Archer, 1989). This leads us to believe, therefore, that previous suggestions of the post-Early Cambrian retreat of *Paleodictyon* into deeper water habitats requires some modification.

The occurrence of *Paleodictyon* in the Georgian Bay Formation demonstrates that at least to the Late Ordovician the operative migratory process was one of expansion rather than retreat. Interestingly, in this context it is notable that Häntzschel (1964) recorded *Paleodictyon* from Cretaceous epicontinental deposits of Westphalia and more recently Hantzpergue and Branger (1991) documented neritic examples from the Jurassic of Aquitaine. Perhaps, therefore, the expansion process continued well into the Mesozoic and additional shallow-water marine examples of *Paleodictyon* await documentation. An alternative scenario is that *Paleodictyon* became re-established in shallow water Mesozoic seas following post-Ordovician retreat into deeper water. However, if in fact the non-marine occurrences reflect amphidromy rather than convergent evolution, this would suggest persistence of shallow-water marine *Paleodictyon* to, at least, the Carboniferous.

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