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Résumé de l'article

Une microbioctnose de l'Ordovicien moyen de filtreurs sessiles du groupe de Trenton dans l'Est du Canada, s'est développée par le biais d'une relation commensale entre un bryzoaire trepostome arborescent et deux taxons de brachiopodes articulés. Un spécimen particulier préserve une communauté de plus de 30 sujets d'œuf et permet d'expliquer la présence de certains brachiopodes pédonculés du Paléozoïque inférieur dans des schistes foncés.

[Traduit par la rédaction]

Mid Ordovician commensal relationships between articulate brachiopods and a trepostome bryozoan from eastern Canada

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A mid Ordovician microcommunity of sessile filter feeders, from the Trenton Group of eastern Canada, developed as a commensal relationship between an arborescent trepostome bryozoan and two taxa of articulate brachiopod. An unusual specimen preserves a life assemblage of over 30 individuals of *Onniella* and provides an explanation for some occurrences of Lower Palaeozoic pedunculate brachiopods in dark shales.

Une microbiocénose de l'Ordovicien moyen de filtreurs sessiles du groupe de Trenton dans l'Est du Canada, s'est développée par le biais d'une relation commensale entre un bryzoaire trépostome arborescent et deux taxons de brachiopodes articulés. Un spécimen particulier préserve une communauté de plus de 30 sujets d'onnies et permet d'expliquer la présence de certains brachiopodes pédonculés du Paléozoïque inférieur dans des schistes foncés.

[Traduit par la rédaction]

INTRODUCTION

The occurrence of pedunculate brachiopods in fine grained sedimentary strata has persistently presented a dilemma to palaeoecologists. A variety of life modes has been presented in explanation. Large terebratulides such as living *Gyrothyris*, *Neothyris* and *Terebratella* (Richardson, 1981a,b) and probably the fossil *Tichosina* (Harper *et al.*, 1995), from the Pleistocene of Jamaica, atrophied their pedicles and pursued a recumbent life strategy resting within the mud. Muir-Wood (1959), however, illustrated the terebratulide *Chlidonophora* attached by a brush-like pedicle to the *Globigerina* Ooze of the Indian Ocean, whereas the thread-like pedicle of deep-sea *Cryptopora* anchored the minute rhynchonellid within a soft substrate and permitted the animal to rise above periodic, dilute turbidity currents (Curry, 1983). Ager (1962) suggested that some small, thin-shelled rhynchonellids found in mudstones, such as the Devonian *Leiorhynchus*, may have been epiplanktonic, attached to floating seaweed whereas, *Gwynia*, the smallest known articulate brachiopod, probably occupied a niche within the interstitial fauna of the substrate (Harper *et al.*, 1996).

We present here evidence of an Ordovician commensal arrangement between an arborescent trepostome bryozoan and a population of the dalmanellid *Onniella*. The articulate brachiopods were associated with the bryozoan by pedunculate attachment and the assemblage provides evidence of a specialized, benthic, epifaunal life strategy for this type of brachiopod commonly found unattached in fine grained, deep-water sediments. Attachment to the bryozoan colony provided anchorage, support and a preferential feeding position far removed from the sediment-water interface. These small brachiopods formed a secondary epifaunal tier of sus-

pension feeders above a soft sediment substrate (Bottjer and Ausich, 1986). Moreover, such tiers were firmly established by the Mid Ordovician.

LOCATION, STRATIGRAPHY AND GEOLOGICAL SETTING

Material described herein was collected from a small working quarry at Château Richer, approximately 22 km northeast of Quebec City, Quebec, eastern Canada (Fig. 1). This quarry is situated in Middle Ordovician (*Orthograptus ruedemanni* Biozone) limestones of the Trenton Group, the youngest carbonate unit in the Taconic foreland basin of southern Quebec (Lavoie, 1995). It represents one of the more northeasterly locations of this lithostratigraphic unit that is more extensively exposed to the southwest in the St. Lawrence Lowlands and then onward into the U.S.A.

In Quebec the Trenton Group has been interpreted as a transgressive continental (Laurentian), platformal margin sequence deposited on a carbonate ramp that initially developed in warm-water tropical and later in temperate conditions (Lavoie, 1995). In the St. Lawrence Lowlands, the sequence is 140 to 220 m in thickness and is represented by an essentially tripartite, but nomenclaturally diverse, succession (for formational terminology see Harland and Pickerill, 1982; Lavoie, 1995). In Quebec City and northeastwards this is represented, from oldest to youngest, by the Pont Rouge, Deschambault and Neuville formations.

The quarry at Château Richer is located within the uppermost Neuville Formation (and in the youngest Grondines Member), where approximately 5 m of thinly interbedded, grey lime mudstones or siltstones and calcareous shales are exposed. There, this sequence has been interpreted as rela-

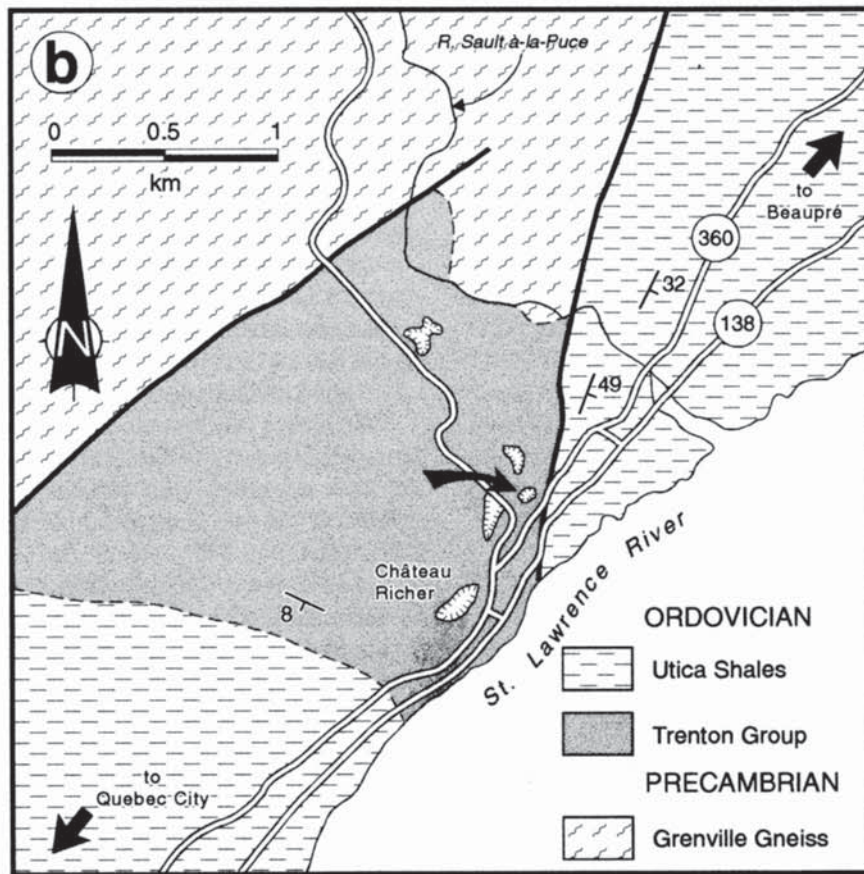
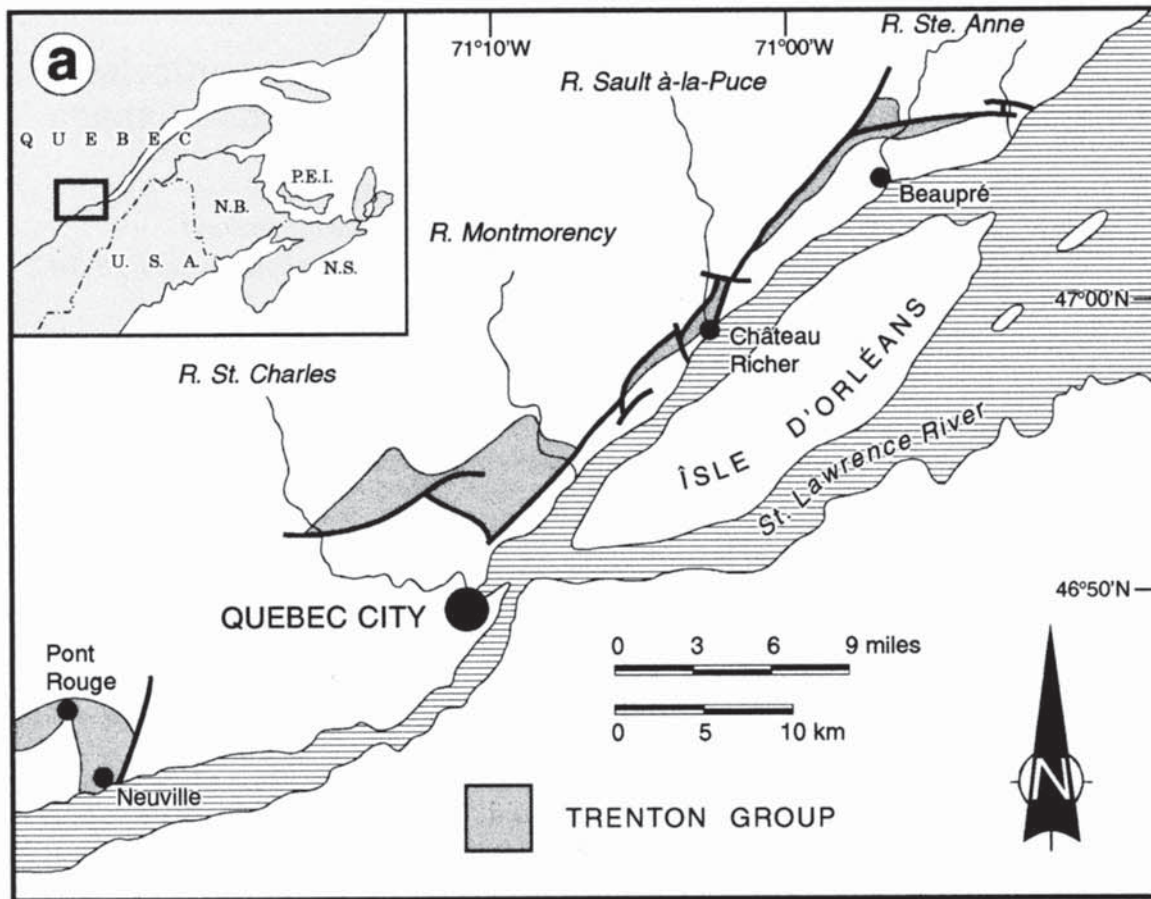


Fig. 1(a). Outcrop map of the Trenton Group adjacent to Québec City; the locality at Château Richer is on the central part of the map, northeast of Québec City. Inset shows geographical location of the area. (b). Detailed geological and location map of the area around Château Richer; the locality is indicated by a curved arrow. Solid black lines in (a) and (b) represent major faults.

tively deep-water in origin, deposited in outer shelf conditions at or, even more likely, below storm-wave base (Harland and Pickerill, 1982), a conclusion also supported by trace fossil evidence (Pickerill and Forbes, 1979). This interpretation is also strengthened by the presence of abundant, parautochthonous, brachiopod-dominated assemblages, virtually complete and articulated examples of crinoids and, albeit rare, examples of annelids (Conway Morris *et al.*, 1982). As further support, the Trenton Group is transitionally overlain by graptolitic strata of the Utica Shales, a black limey shale unit, with thin layers of lime mudstone and siliciclastic siltstone, that is interpreted as an oxygen-stratified basinal deposit (Lavoie, 1995, and references therein).

Limestones of the Trenton Group in the St. Lawrence Lowlands are famous for their richly fossiliferous nature and even preserve examples of linguloid brachiopod pedicles (Pickerill and Forbes, 1978), annelids (Pickerill and Forbes, 1978; Conway Morris *et al.*, 1982) and appendages of several species of trilobites (Raymond, 1920; Størmer, 1939, 1951). However, with the exception of the short report by Harland and Pickerill (1987), commensal relationships such as the one described herein remain undocumented.

COMMENSAL ARRANGEMENTS

Two articulate brachiopod taxa were associated with the branches of the bryozoan (Fig. 2a). The bryozoan is preserved as mainly mouldic material; a more precise identification is not possible. The dalmanellid *Onniella* accounted for virtually all of the more than 30 brachiopod specimens on the block. The specimens are similar to *Onniella multisepta* (Meek); individuals are consistently small, although this may reflect immaturity, with a subcircular outline, relatively well-defined ventral and dorsal muscle scars together with delicate cardinalia. They occur in clusters sporadically developed along the branches of the bryozoan (Fig. 2b). About 20% of the specimens counted appear trapped behind branches of the bryozoan following the postmortem collapse of the colony; some also form small shell hashes under the colony, whereas others may have been dislodged or buried in the sediment after the colony was felled.

Approximately equal numbers of ventral and dorsal valves were counted on the block; all were disarticulated, but the majority were complete and well preserved. The sagittal lengths of 15 ventral and 15 dorsal valves were measured and analyzed; a selection of univariate graphics is presented on Figure 3. The dorsal valves (mean 2.1, variance 0.74) are significantly smaller than the ventral valves (mean 2.4, variance 0.44). Both the ventral and dorsal valve distributions are positively skewed, suggesting the high infant mortality usually associated with life assemblages. Clearly the specimens of *Onniella* were attached in life, by fairly short, robust pedicles; most of the shells are preserved in direct contact with the branches of the bryozoan (Fig. 2a).

The second brachiopod morphotype is represented by a single internal mould of a subquadrate ventral valve with a strongly impressed costellate ornament, characterised by a prominent median rib (Fig. 2b). The valve is an immature

rafinesquinid, slightly dissociated from both the branches of the bryozoan and the clusters of *Onniella*. Rafinesquinids probably possessed active pedicles during early growth stages; however, these were atrophied as adults pursued recumbent life styles within soft substrates. Ambitopic forms such as the rafinesquinids may have taken advantage of this type of substrate to establish the larval shell.

The Château Richer assemblage is immediately overlain by black mudstone, indicating the microcommunity was probably engulfed by a dilute surge of black anoxic mud, rapidly preserving the association, more or less, *in situ*.

DISCUSSION

Articulate brachiopods are relatively rare in Lower Palaeozoic dark shales and siltstones. Traditionally their occurrence has been associated with plankton as epi- or pseudoplankton, living attached to floating organic material such as algae (Bulman, 1964) with a postmortem descent to the seabed prior to burial. Wignall and Simms (1990), in a review of Phanerozoic pseudoplankton, have suggested that the discinoid 'trematids' and the plectambonitoid 'aegiromenids' pursued addressed pseudoplanktonic life strategies. Havlíček (1967) favoured an epiplanktonic life mode for species of *Chonetoidea* and *Sericoidea* that are relatively common in the Ordovician and Silurian of Bohemia. Bergström (1968) reviewed a number of brachiopod assemblages from graptolitic shales dominated by obolids (middle Dicellograptus Shale, Bornholm), sowerbyellids (lower Dicellograptus Shale, Bornholm and the Sularp Shale, Scania) and chonetids (Bringewood Formation, Shropshire). Many of these brachiopods, despite simple deltidodont dentition, were still articulated, suggesting very rapid post- or synmortem burial. Sheehan (1976), however, suggested that these and similar assemblages, preserved in mudstones and shales, may have been attached to biodegradable material, such as plants, rooted to the seafloor.

Nevertheless, a number of unequivocal *in situ*, deep-water, brachiopod-dominated faunas have been documented from fine grained siliciclastic facies. The late Ordovician *Foliomena* fauna (Harper, 1979; Cocks and Rong, 1988) is a sparse, dispersed biota dominated by thin-shelled, minute brachiopods drawn from the main Lower Palaeozoic orders; the dalmanelloid *Dedzetina*, the plectambonitoid *Christiania*, the strophomenoid *Foliomena*, and the athyroid *Cyclospira* are the key elements of this specialized fauna with a near global distribution. The palaeoenvironmental distribution of the fauna was probably related to areas of low oxygen levels with sparse nutrient supplies (Rong *et al.*, 1994).

Jaanusson (1984) developed a model for offshore-onshore, articulate brachiopod distributions based on an analysis of Late Ordovician brachiopod-dominated assemblages from Europe and North America. On the outer shelf and upper slope, associations occur with the plectambonitoids *Chonetoidea* and *Sericoidea* together with lingulates. These associations are probably comparable to the *Foliomena*-type fauna and may have developed adjacent or upslope. In coarser, more nearshore sediments the *Chonetoidea*-*Sericoidea*-type fauna

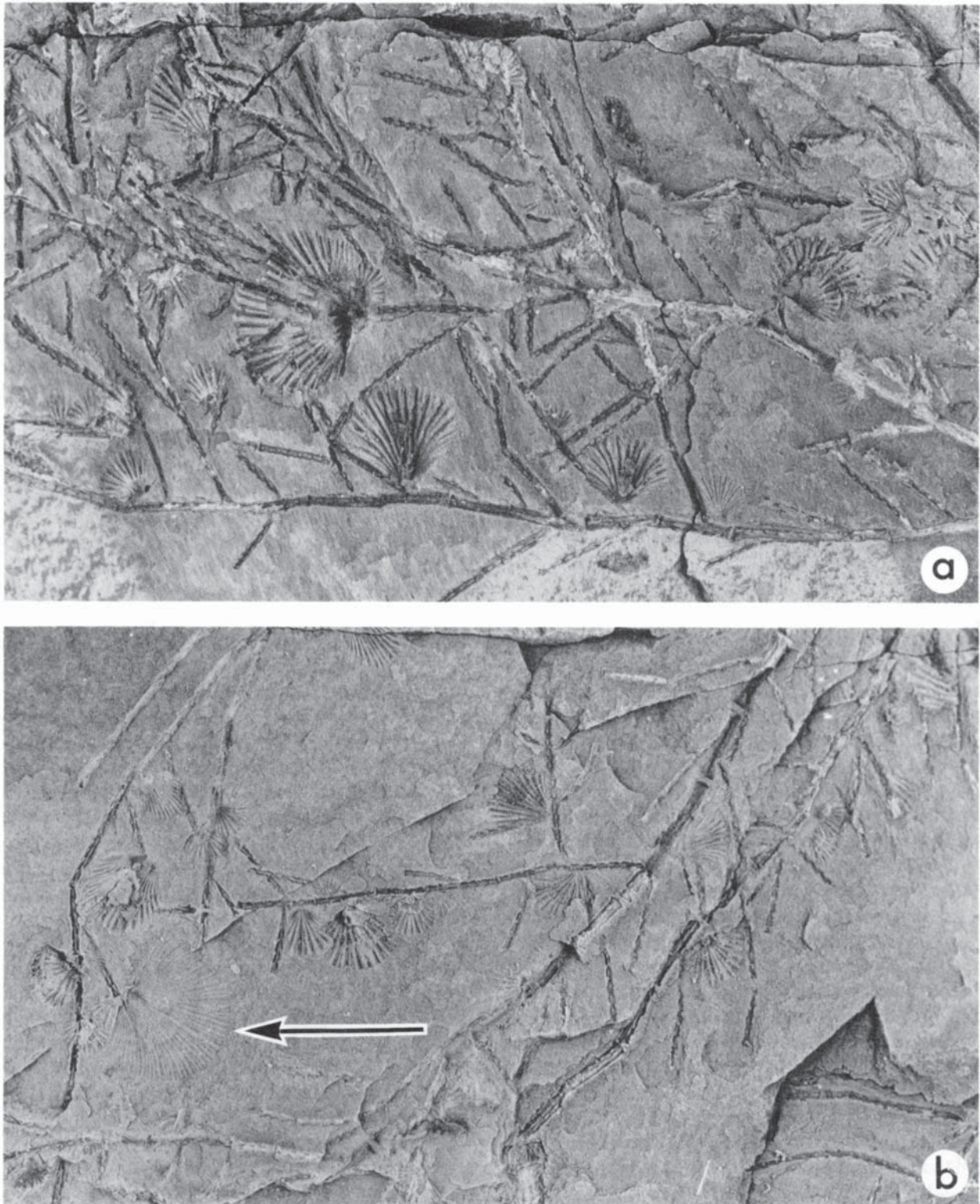


Fig. 2(a). Detail of clusters of *Onniella* attached to the bryozoan (block NBMG 9976 reposit in the New Brunswick Museum). (b). Free-living rafinesquinid brachiopod (bottom left, indicated by arrow) loosely associated on same block with the microcommunity of attached *Onniella*. Magnification of both $\times 8$.

is joined by the dalmanelloid *Onniella*. Generally, *Onniella* is smaller and less common in darker sediments whereas small individuals of *Chonetoidea* and *Sericoidea*, together with micromorphic acrotretoids such as *Hisingerella*, are relatively abundant. For example, transitions from assem-

blages dominated by *Hisingerella* and *Sericoidea* to those with *Onniella* and *Sericoidea* were demonstrated through an upward-coarsening sequence during the late Caradoc in the Oslo basin (Harper *et al.*, 1985). More anoxic conditions may have favoured nonarticulates and small plano-

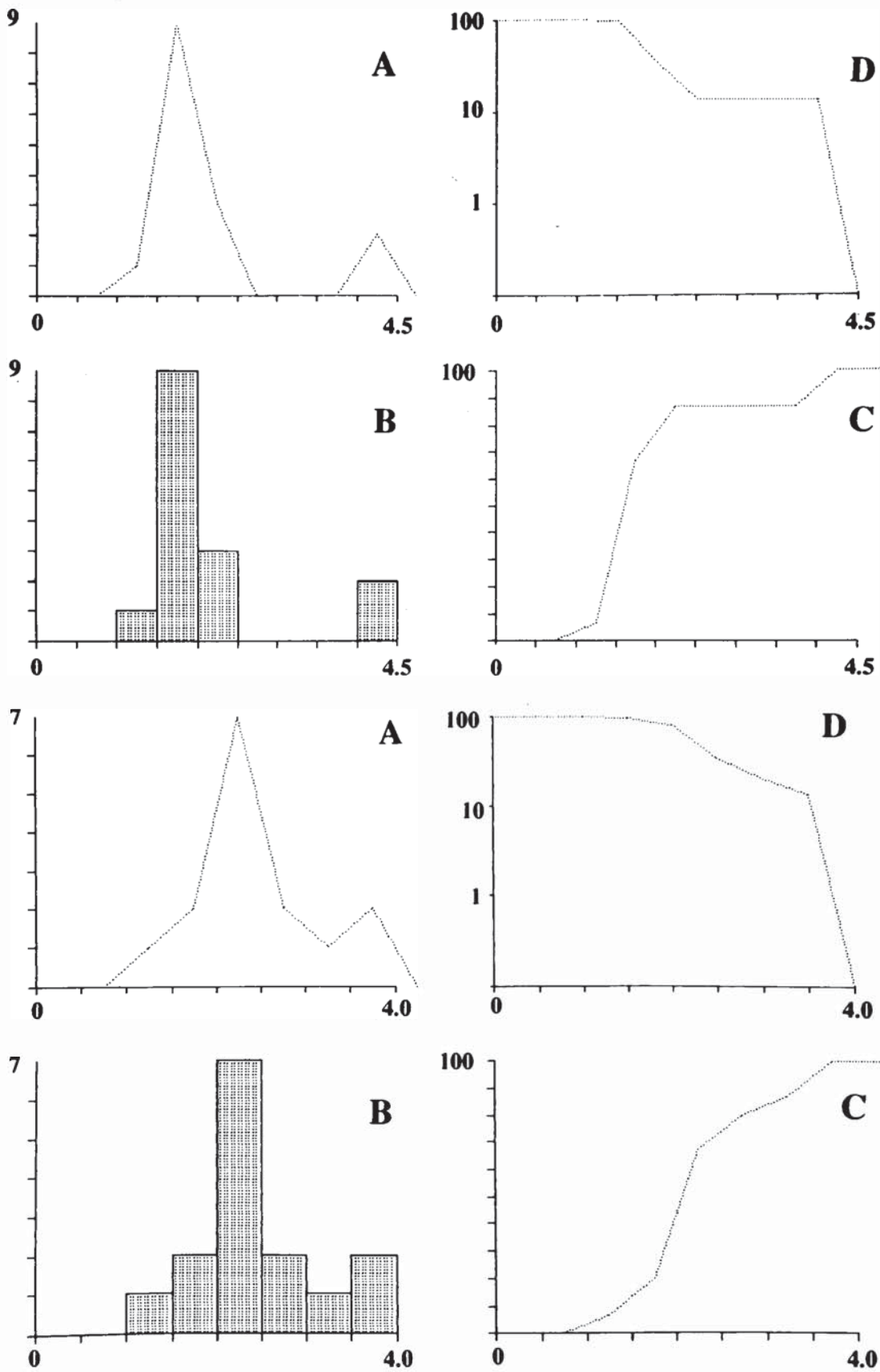


Fig. 3. Univariate graphs of the sagittal lengths of the dorsal (upper) and ventral (lower) valves - (A) Size frequency polygon, (B) Size frequency histogram, (C) Cumulative frequency polygon, (D) Survivorship curve. X axes of all four graphs scaled in mm; Y axes of (A) and (B) represent number of specimens, (C) and (D) as % of total number of specimens.

concavoconvex plectambonitoids. Although the plectambonitoids may have pursued a recumbent strategy, partly within the fine grained substrate (Jaanusson, 1984) and the acrotretoids were possibly part of the interstitial fauna (Bassett, 1984), the life mode of the larger pedunculate articulates, associated with relatively fine sediment, remains an enigma.

Attachment of brachiopods to other organisms is not unusual but direct evidence of attachment is not commonly preserved in the fossil record. The majority of examples reported, however, involve various strophomenides attached by spines to crinoids (Etheridge, 1876; Unklesbay and Niewoehner, 1959; Grant, 1963). Some pedunculate forms, such as the spiriferide *Spiriferina* from the Carboniferous of Scotland (Etheridge, 1876) and the rhynchonellid *Microsphaeridiorhynchus nucula* (J. de C. Sowerby) from the Silurian of Shropshire (Holland, 1971), were demonstrably attached to their hosts by pedicles. Schumann (1969) described attachment by byssus-like pedicles in the Devonian brachiopods *Kiangsiella* and *Uncites*. In addition, Grant (1963) has documented immature growth stages of the productoid *Waagenoconcha*, attached to crinoid stems prior to adult life as a recumbent living within the substrate stabilized by spines. Sandy (1996) has reported the attachment of the atrypoid *Zygospira* to a crinoid stem in the Waynesville Formation of Ohio, extending the record of pedunculate attachment to crinoids back to the late Ordovician. Moreover, the attachment of a specimen of *Paterina* to the enigmatic *Wiwaxia* from the Middle Cambrian Burgess Shale and equivalent deposits (Conway Morris, 1985) suggests this type of attachment has a long history, probably covering the entire Phanerozoic.

Nevertheless, evidence of the attachment of orthide brachiopods is rare. Wright (1968) illustrated a remarkable suite of specimens of the dalmanelloid *Dicoelosia*; five shells were apparently attached, by their pedicles, to a linear organic fragment. The Trenton microcommunity described above, dominated by the pedunculate epifaunal *Onniella*, is a clear example of a commensal arrangement between articulate orthide brachiopods and a bryozoan colony. *Onniella multisecta* is common in the Reedsville Shale and equivalent strata of the northeastern parts of the central Appalachians (Bretsky, 1969). There, *Onniella* occurs with *Sowerbyella* associated with muddy or silty substrates usually in highly concentrated patches. Bretsky (1969, p. 84) suggested *O. multisecta* was directly attached to the substrate or to other shells and non-preserved organics such as worm tubes or algae. The data presented herein firmly supports this interpretation. Lack of suitable taphonomic conditions probably accounts for the scarcity of such specimens displaying commensal relationships elsewhere in the fossil record. Rather, pedunculate brachiopods were detached from their hosts, soon after death, for burial in adjacent sediment.

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