

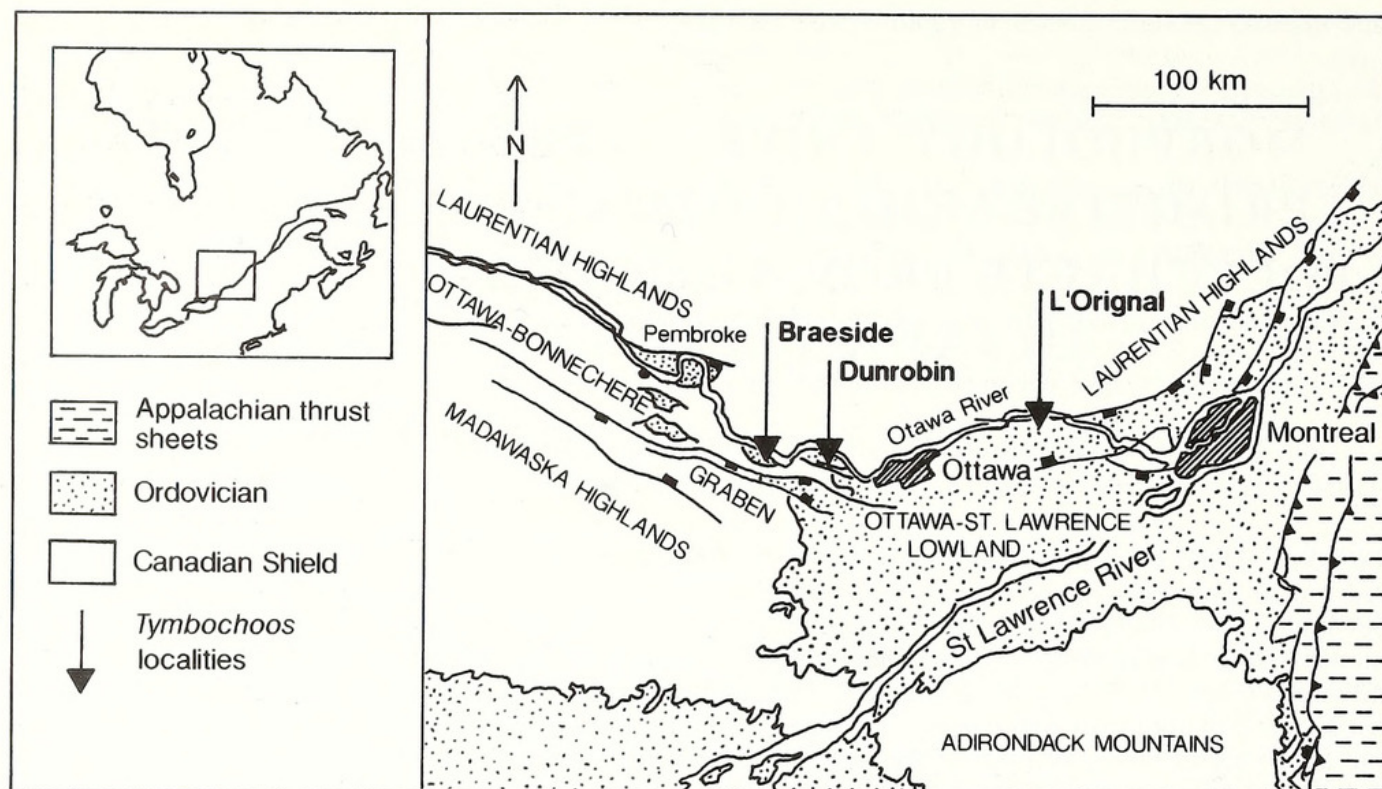
MORPHOLOGY AND PALAEOECOLOGY OF A PRIMITIVE MOUND-FORMING TUBICOLOUS POLYCHAETE FROM THE ORDOVICIAN OF THE OTTAWA VALLEY, CANADA

by H. MIRIAM STEELE-PETROVICH and THOMAS E. BOLTON

ABSTRACT. Build-ups of the calcareous tube, *Tymbochoos* (gen. nov.) *sinclairi* (Okulitch), occur in mid Ordovician limestones of the Ottawa Valley; the oldest previously known build-ups of calcareous tubes are Devonian. The *Tymbochoos* build-ups occurred as elongate dune-shaped structures in tidal channels on intertidal flats, and as small isolated pillow-shaped structures on near-shore subtidal shoals. Clustered tubes radiated horizontally from small attachment areas and then grew vertically. Individual tubes widened quickly to a diameter of about 1 mm and then grew cylindrically; irregularly spaced concentric constrictions of the tube wall developed in places into thin anteriorly directed internal collars. Growth forms include (1) a framework of concentrated clumps of densely packed, long vertical tubes, found only in the dune-shaped structures, (2) a sparser concentration of clumps with more loosely packed shorter vertical tubes in the pillow-shaped structures, and (3) scattered tube aggregates. *T. sinclairi* was probably a primitive suspension-feeding polychaete that fed with short tentacles and was supported by its setae-bearing parapodia against the irregularities of the inner tube surface. Few other species were associated with these Ordovician tube build-ups; exploitation of the intertube environment probably began at the end of the Cretaceous.

BUILD-UPS with frameworks dominated by calcareous tubes are rare in the fossil record. The oldest previously reported tube-supported framework is Devonian (Beus 1980), but its taxonomic affinity is uncertain (ten Hove and van den Hurk 1993). Several Carboniferous reefs have tubicolous frameworks, considered to be of vermetid origin (Leeder 1973; Burchette and Riding 1977; Wright and Wright 1981; Weedon 1990). Although build-ups supported by serpulid tubes have been documented from rocks at the Triassic-Jurassic boundary, they remain fairly uncommon through the Tertiary (ten Hove and van den Hurk 1993). With the discovery of well-defined build-ups in the Ottawa Valley, Canada, the geological range of confirmed build-ups that are supported by calcareous tubes has been moved back to the early mid Ordovician. These Ordovician build-ups and the environments they occupied are similar in many ways to those of Recent serpulids and vermetids; the similarities imply both considerable evolutionary and ecological convergence and conservatism of calcareous tube-dwelling organisms over the past 450 million years.

The build-ups of this study occur as dune-shaped structures, both in the wall and on the top surface of a quarry at L'Orignal, as a field of well exposed small pillow-shaped structures at Braeside, and as poorly exposed mounds on a crumbly exposure face at Dunrobin (Text-fig. 1); small scattered clumps of tubes are relatively rare. Detailed knowledge of the environments of deposition (Steele-Petrovich 1984, 1986, 1989, 1990) and the exceptional preservation of numerous tubes have enabled the detailed studies of taxonomy, morphology and palaeoecology, presented here, of this Ordovician tube-building organism. This species, until now classified as a rugose coral, *Fletcheria sinclairi* (Okulitch 1937; Wilson 1948), is here reassigned to *Tymbochoos*, a new genus, which is inferred to be a primitive polychaete.



TEXT-FIG. 1. Map of Ottawa Valley showing *Tymbchoos* localities.

STRATIGRAPHY AND GEOLOGICAL SETTING

The tubicolous build-ups of this study occur in limestones of Blackriveran age, assigned traditionally to the Pamela and Lowville formations (e.g. Wilson 1946), and more recently (e.g. Williams and Telford 1986) to the Shadow Lake and Gull River formations of Liberty (1964), and to the B, C and β lithostratigraphical units of Steele-Petrovich (1986, 1989; Text-fig. 2).

The sediments at Braeside and Dunrobin accumulated in a shallow quiet tropical lagoon behind a lime-mud bank (Steele-Petrovich 1984, 1989); there is evidence that the bank and lagoon developed within a narrow gulf, and migrated with the transgressing sea up a pre-existing rift valley that preceded the present Ottawa-Bonnechere Graben. In contrast, the sediments at L'Original were deposited on a normal level bottom within the Ottawa Basin (Steele-Petrovich 1989).

ARCHITECTURE OF THE BUILD-UPS

Dune-shaped mounds

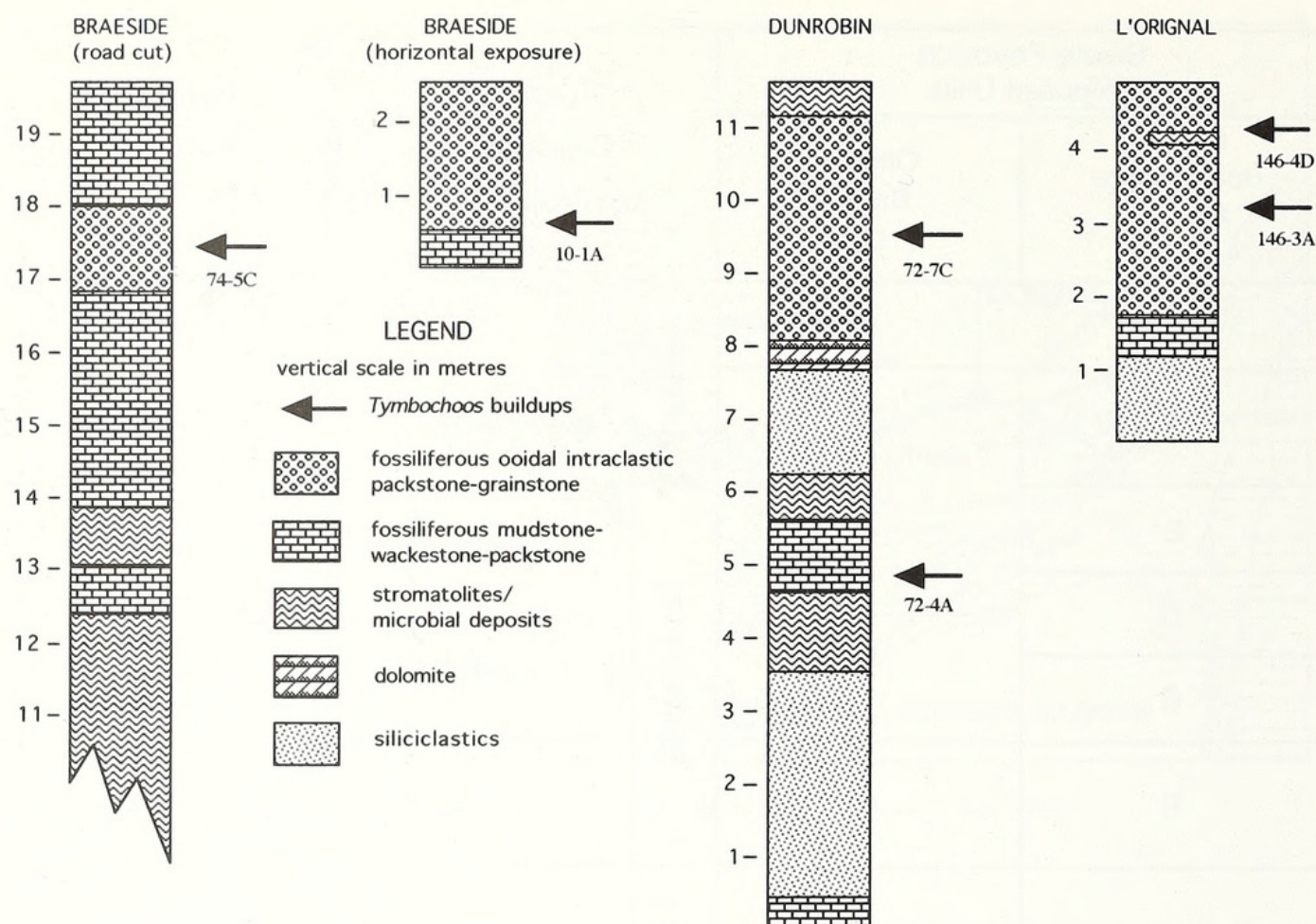
Dune-shaped mounds of *Tymbchoos* occur at two stratigraphical horizons in a small quarry near L'Original (Text-fig. 3). The upper horizon is exposed both in the quarry wall and on the table rock at the top of the quarry (Text-fig. 4A). Forty-eight mounds, somewhat reminiscent of Andrews' (1964) subfossil serpulid reef fields from Baffin Bay, Texas, occur at the top of the south side of the quarry, in an area of about 20×150 m; their lengths are generally 1.5–3.0 m but up to 5.0 m, length-to-width ratios are 1.5–2.5. Actual mound heights are generally 0.45–0.50 m; heights above the contemporary intermound sediment vary from about 0.10–0.35 m, and are comparable to those of many Recent and fossil serpulid build-ups (e.g. Andrews 1964; Braga and Lopez-Lopez 1989; ten Hove and van den Hurk 1993). The mounds trend north-north-east, most within azimuths 20 – 35° (Text-fig. 5). They are asymmetrical in cross section, with the west-north-west side generally sloping

Steele-Petrovich Proposed Units			Traditional Classification (e.g. Wilson 1946)	Williams and Telford (1986) (after Liberty 1964)
Ottawa- Bonnechere Graben (1986)	Ottawa Basin (1989)			
		Trenton		
F	δ	Black River	Rockland	Bobcaygeon
E			Chaumont	
D				
C	γ		Lowville	Gull River
B	β		Pamelia	Shadow Lake
A	α	Chazy	Rockcliffe	Rockcliffe

TEXT-FIG. 2. Middle Ordovician stratigraphy of the Ottawa Valley.

between 30° and 60° and the opposite side sloping at less than 20° (Text-fig. 4A); smaller disconnected mound patches commonly occur along the periphery of the more gently sloping side. The mound surfaces are commonly knobby or ridged, with shallow relief. The lower mound horizon can be seen only on a small weathered portion of the quarry wall and on a few square metres of horizontal shelf; these exposed mounds are rounded and appear to be almost symmetrical dune-shaped structures (Text-fig. 6A-B), about 0.7 m across, 0.4 m high with height about 50 mm above the contemporary sediment surface.

Tymbochoos sinclairi was a suspension feeder, as implied by the current-controlled dune-shaped mounds. Orientation of the asymmetrical mounds can be interpreted by analogy with Recent serpulid build-ups, studied by Behrens (1968), that encrust the insides of rectangular water-intake tunnels of an electric power plant in Corpus Christi, Texas. This Recent encrusting growth develops shapes and orientations similar to those of ripple marks formed in non-cohesive sediment: the structures are perpendicular to the current, with gentle and slightly rounded up-current slopes and steep down-current slopes. Although both of these forms have the same asymmetrical shape, the Recent structures, with wavelengths of 0.10–0.15 m, heights of 10–20 mm, and crest lengths of 0.10–0.20 m, are considerably smaller than the asymmetrical mounds of this study. The similarity in form suggests that the asymmetrical *Tymbochoos* mounds developed where the dominant tidal current (probably the incoming current) flowed west-north-westwards; the symmetrical mounds probably formed where incoming and outgoing current strengths were similar.



TEXT-FIG. 3. Stratigraphical sections as measured at each locality, showing Steele-Petrovich locality numbers for the *Tymbochoos* occurrences.

Pillow-shaped structures

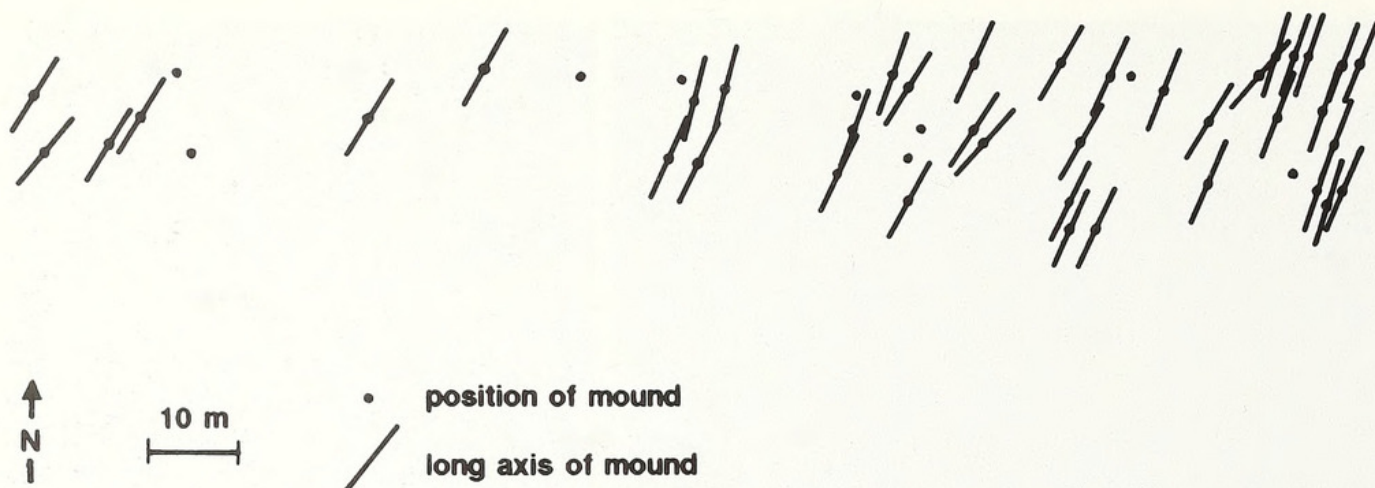
Limestone 'pillows' are concentrated on what appears to be a single bedding plane that crops out at several locations near Braeside (Text-fig. 1). The structures are sub-circular to elliptical in plan, usually 0.10–0.25 m across and up to 0.4 m long, flat on the bottom and flat to slightly domed on top, with sharply defined rounded to angular edges (Text-fig. 7); their thickness is generally about 100 mm, with 30–50 mm exposed above the bedding plane (Text-fig. 7D). In rare cases the upper surfaces of the 'pillows' are pitted and appear to have been bored (Text-fig. 7C). Although a bulldozer had disturbed the exposures, 14 'pillows' were in place in an undisturbed area measuring about 3×2 m, and were generally spaced no more than 0.3–0.5 m apart; some were almost touching each other and in several cases two or three had grown together.

Other mounds

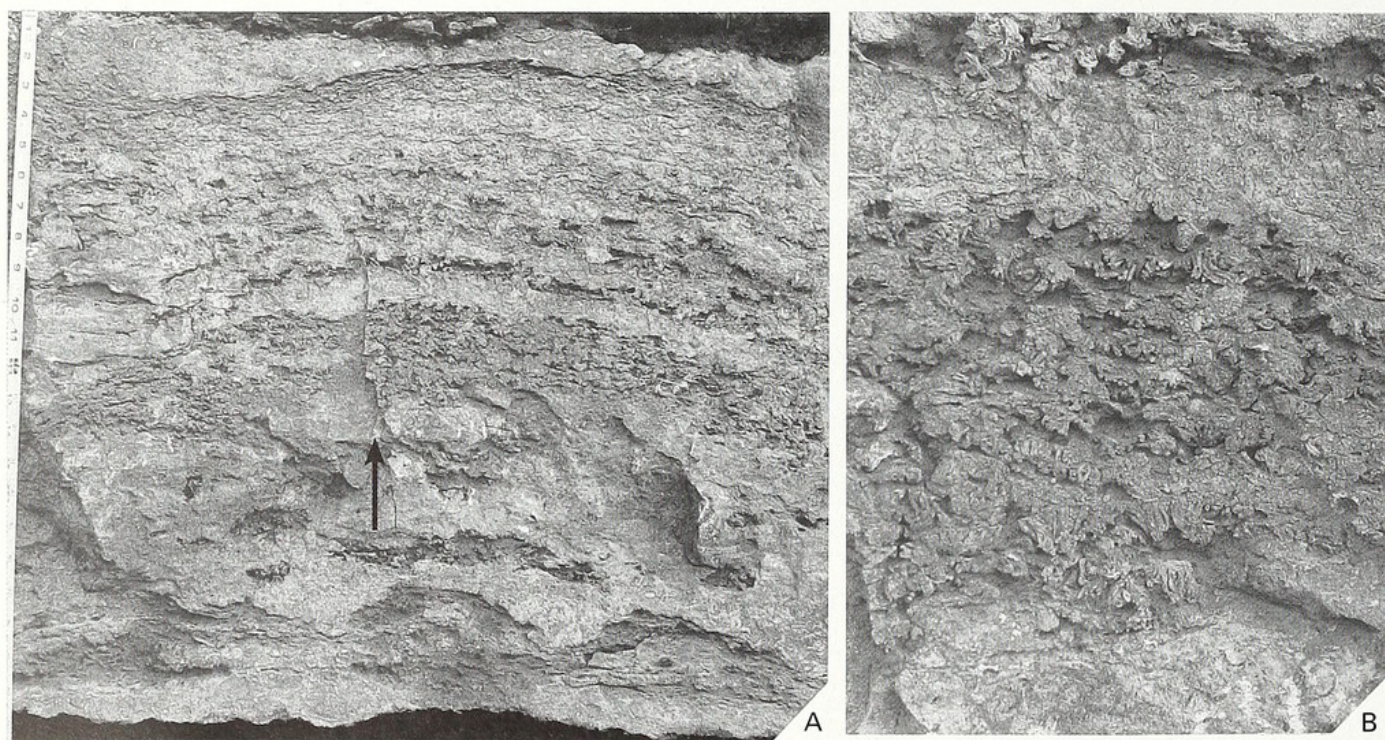
Clusters of mounds are poorly exposed and/or poorly preserved at several horizons in a road-cut and associated narrow ditch near Dunrobin (Text-fig. 1); those in the ditch have been sheared off horizontally, and those in the road-cut occur in a crumbly part of the section and are poorly defined. These build-ups vary considerably, from small buttons to poorly defined masses nearly one metre across, from regular saucer or mound shapes to build-ups with irregular projections, and from isolated mounds to those that grew together, both laterally and vertically. Because of poor



TEXT-FIG. 4. Macrostructures of asymmetrical, dune-shaped mounds from near L'Orignal (see Text-figure 3 for identification of S-P locality numbers). A, view down the crest of an individual mound at top of south end of quarry. Slope of right (i.e. east-south-east) flank about 20° ; slope of left (west-north-west) flank about 50° . Surface irregular due to shallow channels. Small disconnected patches of mound along periphery of gently sloping flank. Inferred current direction from right. Length of tape case 65 mm. B, GSC hypotype No. 115517; hand specimen showing horizon of densely packed, long vertical tubes between horizons of densely packed horizontal tubes; $\times 1$. C, GSC hypotype No. 115518; hand specimen from scree at south end of quarry (S-P Locality No. 146), showing relatively densely packed tubes with concentric crenulations and, in some cases, longitudinal ridges; $\times 6$. D, top surface of a mound showing scattered clumps of radiating, mainly horizontal tubes. Scale in inches. Photographs A-B and D taken at S-P Locality No. 146-4D (GSC No. O-104069).



TEXT-FIG. 5. Map showing relative positions and alignment of asymmetrical, dune-shaped mounds at top of south side of quarry, near L'Orignal.

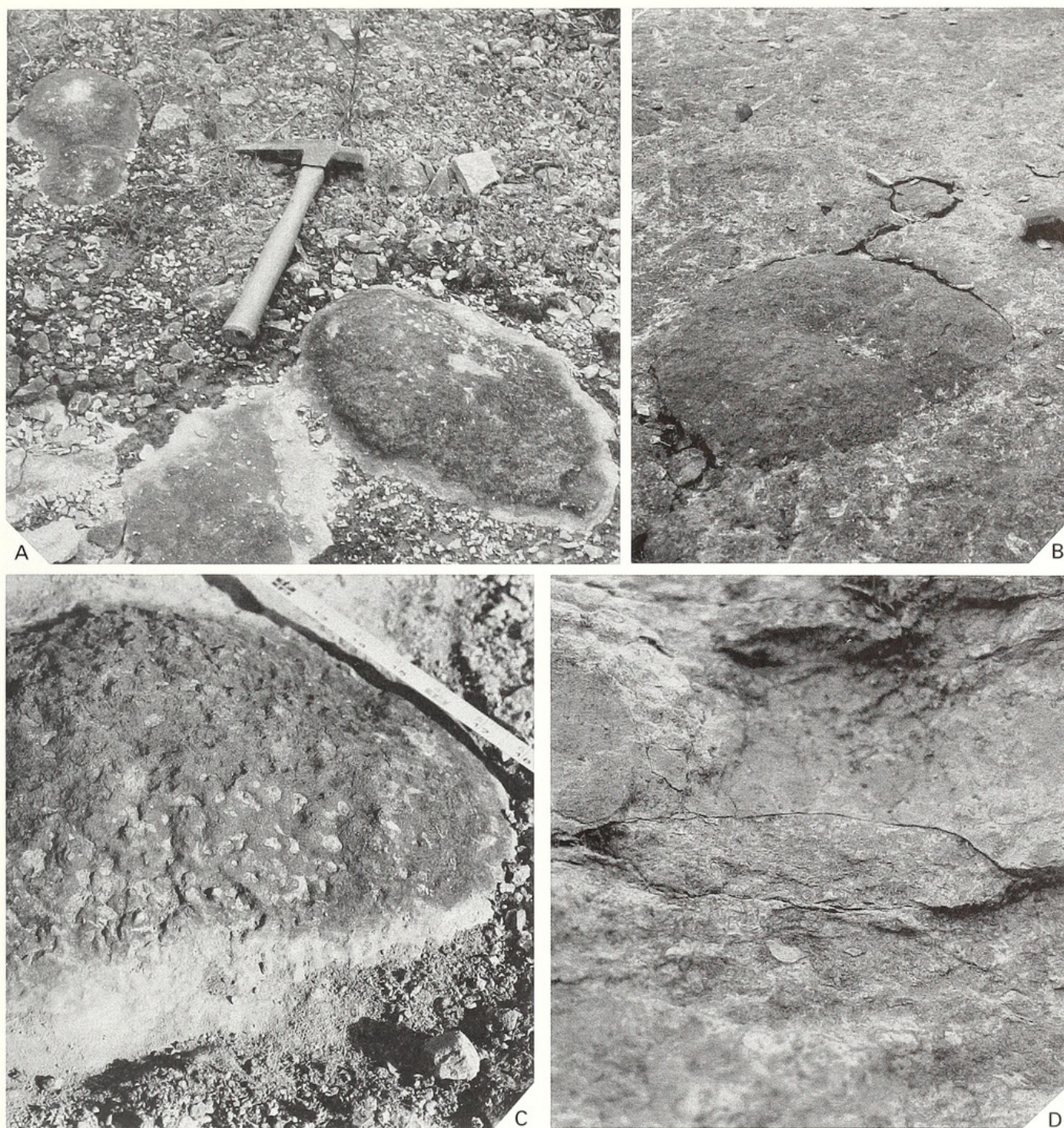


TEXT-FIG. 6. Macrostructures of symmetrical, dune-shaped mounds formed by *Tymbochoos*, located near L'Orignal (see Text-figure 3 for identification of S-P locality numbers). A, section through lower mound horizon in west-facing quarry wall, showing individual growth horizons of tubes. Arrow marks position of left side of B. Scale in inches. S-P Locality No. 146-3A (GSC No. O-104065). B, enlargement of part of A, to right of arrow; relatively dense, subvertical tubes in radiating clumps that are emphasized by differential weathering, between horizons of densely packed, horizontal tubes that have not been emphasized by weathering.

preservation and exposure, these mounds are of interest primarily for the environment that they occupied.

Isolated tube aggregates

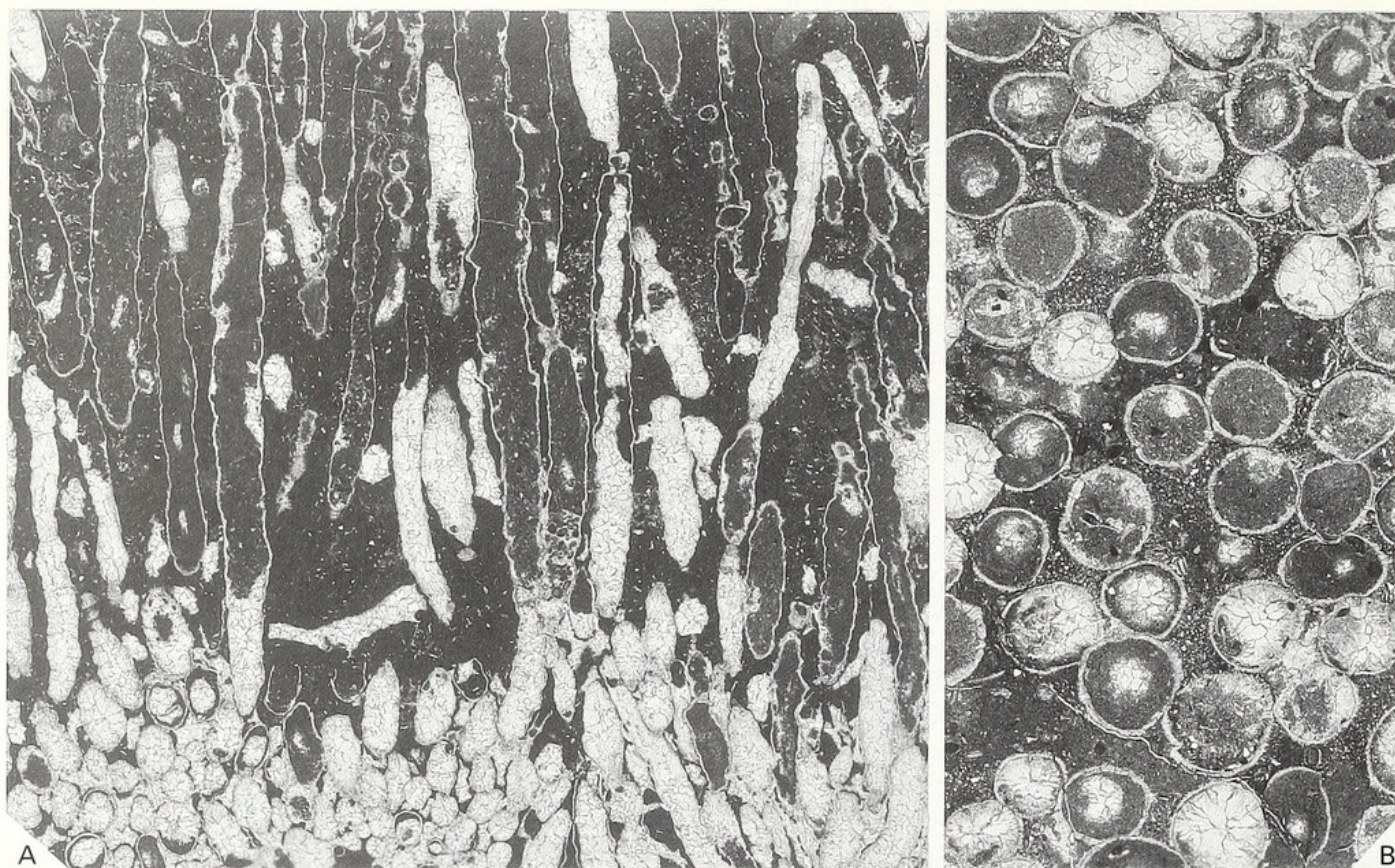
Isolated small clumps of *Tymbochoos* tubes occur in living position, often close to build-ups.



TEXT-FIG. 7. Macrostructures of pillow-shaped mounds from Braeside (see Text-figure 3 for identification of S-P locality numbers). A–B, on disturbed (A) and undisturbed (B) bedding planes, showing sub-circular and elliptical shapes in plan view. Length of hammer 0.35 m (only partially visible in B); S-P. Locality No. 75-1A (GSC No. O-106469) (lateral equivalent of 10-1A). C, enlargement of far side of large 'pillow' in figure A showing pitted surface; scale in inches. D, vertical section through small 'pillow' (about 40 mm thick) showing its flat bottom, slightly domed top and sharply defined, angular edges; S-P. Locality No. 74-5C (GSC No. O-105755).

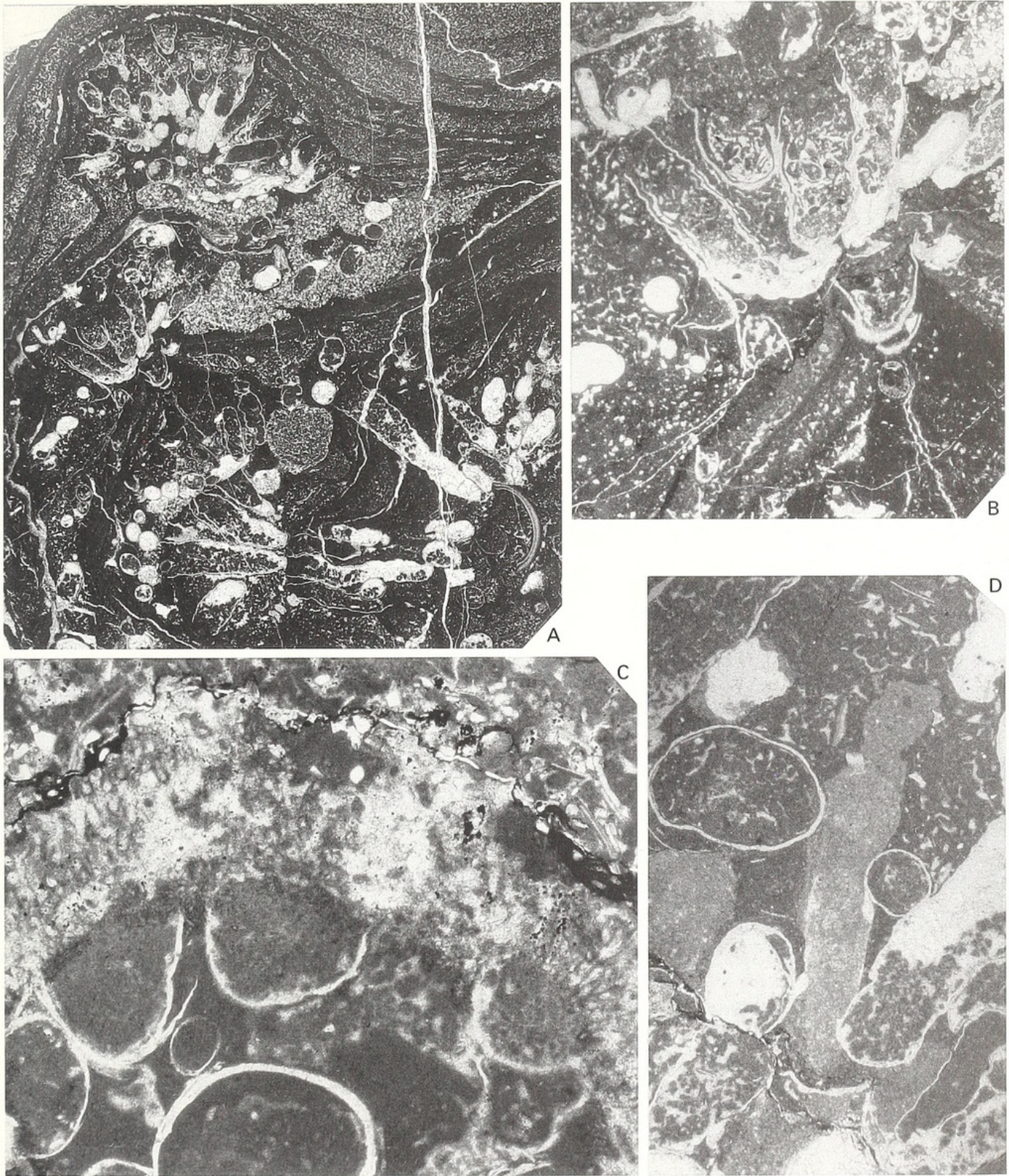
FORM AND GROWTH OF THE TUBES

The tubes of *T. sinclairi* (Text-figs 8, 9A–B, 10–11) are circular in cross section and expand very quickly from *c.* 0.12 mm at the base to a mature size of generally 0.95–1.30 mm (maximum

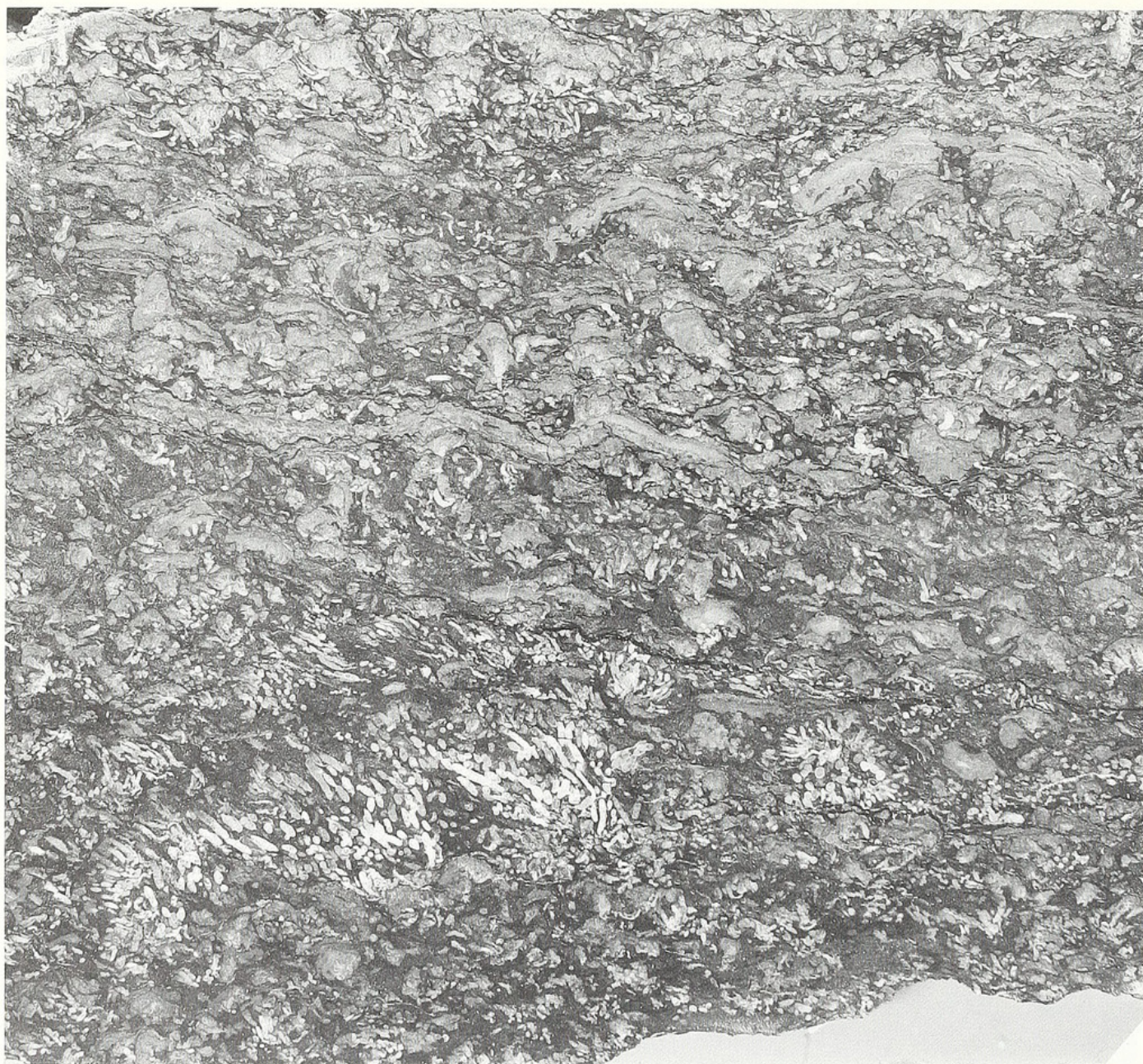


TEXT-FIG. 8. Photomicrographs of symmetrical, dune-shaped mounds from near L'Original; S-P Locality No. 146-3A (GSC No. O-104065) (see Text-figure 3 for identification of S-P locality numbers). A, GSC hypotype No. 115519; vertical section showing long tubes and dense, subparallel vertical growth of framework-type structure. Horizontal radiating growth at base appears to be from three closely packed tube aggregates; vertical tubes show fine tube walls with concentric constrictions; $\times 5$. B, GSC hypotype No. 115520; horizontal section through framework-type structure showing dense packing and sub-circular cross section of mature tubes; $\times 10$.

1.50 mm); subsequent growth produced straight to slightly sinuous, cylindrical tubes. The circular cross section is seldom distorted significantly by contact with other tubes (Text-fig. 8B). Unlike some Recent serpulid species, which share walls in the area of contact (Hartmann-Schröder 1967), contiguous individuals of *T. sinclairi* each appear to have produced a complete tube; apparent sharing of walls, where it occurs, appears to result from selective dissolution of a part of one tube. Tube-wall thicknesses vary greatly (0.02–0.12 mm) in a manner that is unrelated to tube diameter (compare Text-figs 8–9, 11) and is probably due to diagenesis. In rare cases, longitudinal ridges occur on the weathered exteriors of *T. sinclairi* tubes (Text-fig. 4c). In thin section these ridges have been seen only on specimens with unusually thin, apparently unaltered, walls (Text-fig. 11B); about 20 fine ridges can be spaced somewhat unevenly around a tube, or several can occur on only a part of the surface, suggesting that certain ridges were obliterated by diagenesis. However, as considerable variation in tube morphology of another group of polychaetes, the Recent serpulids, can be associated with different growth stages (Hartmann-Schröder 1967) and environmental changes (ten Hove and van den Hurk 1993), one cannot dismiss the possibility that variation in ridging in the *T. sinclairi* tubes is primary. Most of the studied tubes are constricted concentrically at semi-regular intervals (Text-figs 8A, 9B, 11A, C), which results in unevenly corrugated inner and outer surfaces. In places these constrictions have developed into thin, anteriorly directed, internal collars (Text-fig. 11C) that result from the inward growth of the leading edge of the tube. These collars do not occur in all tubes; when present, they can encircle the whole tube and be relatively regularly spaced at about 0.4 to 0.6 mm intervals, or they can be well defined on only a part of the



TEXT-FIG. 9. Photomicrographs of asymmetrical, dune-shaped mounds from near L'Orignal (see Text-figure 3 for identification of S-P locality numbers). A, GSC hypotype No. 115522; S-P Locality No. 146-4D (GSC No. O-104069); vertical view of small scattered radiating *Tymbochoos* clumps growing on and overgrown by stromatolitic laminae; $\times 4.95$. B, enlargement of centre left of A showing attachment of small isolated radiating clump of tubes to firm stromatolitic surface; $\times 13.85$. C, GSC hypotype No. 115521; S-P Locality No. 146-4B (GSC No. O-104067) (lateral equivalent of 146-4D); vertical section showing small *Tymbochoos* clump in early stage of tube growth with filamentous microbial overgrowths; $\times 32.65$. D, GSC hypotype No. 115523; vertical section showing *Tymbochoos* tubes in burrowed microbial deposits; $\times 13.85$; S-P Locality No. 146-4D (GSC No. O-104069).



TEXT-FIG. 10. GSC hypotype No. 115524; polished vertical surface from the upper part of an asymmetrical, dune-shaped mound showing a few radiating clumps of *Tymbochoos* tubes near the base, and toward the top an increase in abundance of isolated horizontal tubes and wavy and mounded microbial growths; $\times 0.99$; S-P Locality No. 146-4D (GSC No. O-104069) (see Text-figure 3 for identification of S-P locality numbers).

tube and pass into simple constrictions on the opposite side. The degree to which these differences are primary or an artefact of preservation is difficult to determine. After a collar had formed, tube growth resumed on the outside of the tube below the collar and then enclosed the collar region. Unlike the tubes of most Recent species of serpulids and vermetids (ten Hove and van den Hurk 1993), the tubes of *T. sinclairi*, with intermittent periods of tube constriction at the anterior ends, could not have been closed by an operculum; even a flexible fleshy operculum would probably have caught on the constrictions as it was withdrawn into the tube (H. A. ten Hove, pers. comm. 1996).

Tubes typically grew in clumps, which have the same pattern of growth in the different kinds of build-ups. Most clusters were probably anchored to a firm base, such as a shell fragment, ooid, intraclast, stromatolitic hardbed, or upper tip of a clump of previously abandoned tubes (Text-figs 9A–B, 11A, C). Many Recent serpulids attach themselves to fallen tube fragments of their own species

(Bosence 1979; ten Hove and van den Hurk 1993), but broken fragments of *T. sinclairi* are rare. This scarcity can be attributed to several factors: to negligible bioerosion during the Ordovician, compared with the Recent (cf. Bosence 1979; ten Hove and van den Hurk 1993), to the support given to the tubes by penecontemporaneous sediment filling the intertube space (cf. Straughan 1972; ten Hove and van den Hurk 1993), and to microbial overgrowth of the tubes shortly after the animal's death (discussed later). Attachment areas of the clumps are invariably small, almost certainly because of both the gregarious settling of the larvae and the scarcity of suitable substrate, as analogies with Recent serpulids suggest (cf. Bosence 1979; ten Hove 1979; ten Hove and van den Hurk 1993); available hard particles, other than the worm tubes, were very small and relatively scarce in *Tymbochoos*-inhabited environments, and only the initial settlers in a clump appear to have been attached to a firm external base. Succeeding spat settled at the base of the established tubes; tubes within a clump grew sub-horizontally and radially out from the initial attachment area, and after a sufficient base had been established, they turned upward and grew vertically (Text-figs 8A, 11A, C). There is no evidence of spat having settled on the vertical walls of growing tubes, as with some Recent serpulids (cf. Hartmann-Schröder 1967; ten Hove and van den Hurk 1993), possibly because periodic larval production more-or-less coincided with the death of the previous generation, as in some Recent serpulid communities (cf. Behrens 1968; Straughan 1972) (discussed below), and/or because conditions that were suitable for larval settlement lasted for only a short time after initial settlement.

INTERNAL STRUCTURES OF BUILD-UPS

Internal structures of the different kinds of *T. sinclairi* build-ups differ considerably in maximum density of clumps of tubes, tube density within the clumps, maximum tube length, and concentration of associated microbial growth/binding. Clumps that form the 'pillow' structures are usually relatively widely spaced and small, consisting of a comparatively few short tubes (Text-fig. 11A, C-D), which rarely reach more than 4–8 mm above the base. In contrast, a dense framework structure of tubes dominates the dune-shaped mounds (Text-figs 4B–C, 6, 8), except near the tops of at least the asymmetrical mounds, where stromatolitic growths dominate (Text-fig. 10).

Tube density

The framework structure consists of relatively long horizontal and vertical (or sub-vertical) tubes, commonly in well-differentiated rows (Text-figs 4B, 6, 8A). At densest packing, the vertical tubes are several tens of millimetres long, occupy at least two-thirds of any horizontal cross sectional area, and appear to be more-or-less subparallel throughout and in contact with one or more other tubes along much of their lengths (Text-figs 4B, 8). The strength provided by tube contact in these Ordovician structures must have outweighed the competitive disadvantage of not having had a regular separation of feeding apparatuses. In contrast, many Recent serpulids have both equal spaces between tube apertures (Bosence 1979; ten Hove and van den Hurk 1993) and lengthwise contact with other tubes (ten Hove, pers. comm. 1996), thereby combining strength with feeding effectiveness. A somewhat flaring upward growth in the Recent serpulids results in intertube space that is subsequently colonized by younger tubes, producing a closely packed tube structure posterior to the evenly spaced apertures (compare text-figs in Bosence 1973, 1979 and those in ten Hove and van den Hurk 1993).

As tube growth in Recent serpulids accounts for most of their expended energy (Dixon 1980), maximum tube growth must occur under optimum environmental conditions (cf. Hartmann-Schröder 1967). High larval survival rates, which also depend on favourable conditions (cf. Straughan 1972), are necessary for the growth of densely packed tubes (cf. Hartmann-Schröder 1967). By analogy, the framework structure of *T. sinclairi*, with its long densely packed tubes, must have developed when conditions were particularly favourable, and the more sparsely distributed clusters with short tubes grew in poorer conditions. The increase in microbial growths with decrease

in tube density (discussed below) supports the argument that sparse tube growth formed under poorer conditions.

Death and replacement

Intermittent mass death and subsequent replacement by another generation of tubes occurred in both dense and sparse populations of *T. sinclairi*: clumps of tubes originated at a single horizon and grew to approximately the same height (Text-figs 4B, 6, 11A), indicating that the clumps developed from the same spatfall, grew at about the same rate, and died *en masse*. Where clumps and tubes are relatively widely spaced, new growth commonly occurred on a thin sediment layer that covered the death horizon. In contrast, the dense framework structure has alternating horizontal and vertical growth in contiguous layers, commonly several tens of millimetres thick (Text-figs 6B, 8A). A similar growth pattern of dense tubes is found in the sub-Recent serpulid patch reefs of Baffin Bay (cf. Andrews 1964) and in the fouling structures within the water-intake tunnels in Corpus Christi (cf. Behrens 1968); in the latter, each couplet represents an annual cycle of growth. Laboratory studies indicate that growth rates of the serpulid tubes in the first two to four weeks after settlement of the spat are ten to twenty times greater than in later life, leading Behrens (1968) to suggest that the newly settled worms crowd out and kill the previous generation. However, a more likely interpretation is that the adult worms die each year immediately after reproducing. A similar growth pattern in the framework structure of *T. sinclairi* suggests a comparable type of replacement.

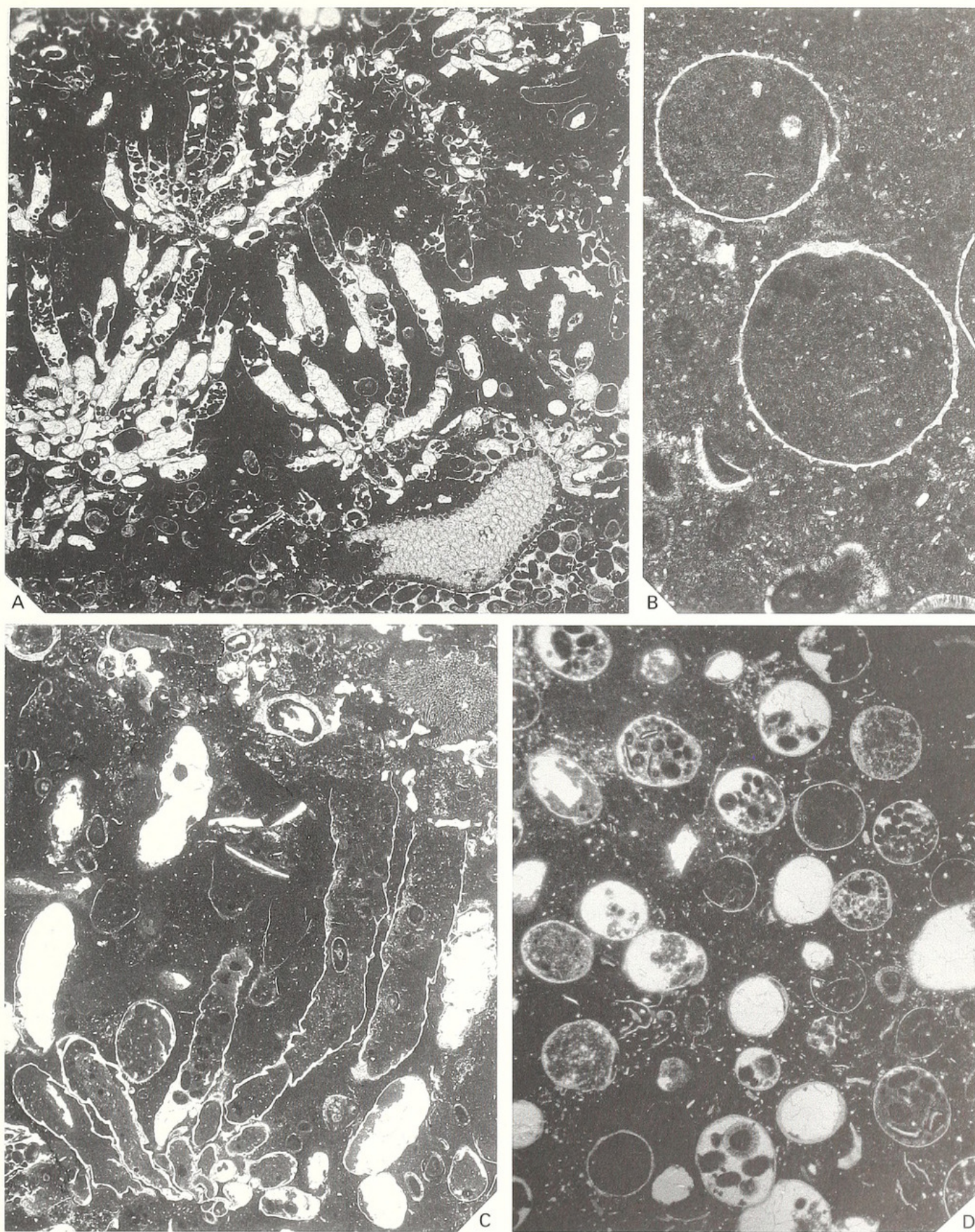
Intertube burrowing

A penecontemporaneous carbonate mud, commonly with scattered peloids and ooids, occurs between the tubes in *T. sinclairi* build-ups (Text-figs 8–9, 11). Horizontal, vertical and oblique burrows (diameters 0.8–1.2 mm) are common in association with microbial growths amongst the sparsely distributed clusters of tubes in the asymmetrical dune-shaped mounds (Text-fig. 9D). Well defined horizontal burrows (about 0.5 mm diameter) and poorly defined swirls occur more rarely and in the absence of microbial growths within the compact framework structure. In most cases, poorly defined, almost ethereal swirls are the only evidence of burrowing within the ‘pillows’.

Microbial growths

Stromatolitic growths, as well as non-stromatolitic microbial growths with filamentous, vermiform, and clotted textures, occur only with sparsely distributed tube clumps (Text-figs 9–10, 11c). There is no evidence of microbial development associated with the dense framework structure that dominates the dune-shaped mounds (Text-fig. 8), although abundant stromatolitic growth occurs

TEXT-FIG. 11. Photomicrographs of pillow-shaped mounds from Braeside (see Text-figure 3 for identification of S-P locality numbers). A, GSC hypotype No. 115525; S-P Locality No. 10-X (GSC No. O-105757) (lateral equivalent of 10-1A); vertical view showing (1) relatively widely-spaced tube aggregates with radiating, sub-horizontal basal tube growth and relatively short vertical tube growth; (2) several tube aggregates growing from a single horizon to approximately the same height and being replaced subsequently by another aggregate that grew directly on the abandoned tubes; (3) tube aggregate (lower right) growing on a trepostome bryozoan fragment; $\times 5$. B, GSC hypotype No. 115525; same locality as A; horizontal section through two *Tymbochoos* tubes showing thin shells with radial projections (representing longitudinal ridges) on the outer surfaces; $\times 40$. C, GSC hypotype No. 115526; S-P Locality No. 10-1A (GSC No. 90071); vertical views of tube aggregate with radiating, sub-horizontal basal tubes and relatively short vertical tubes; vertical tubes with fine tube walls, concentric constrictions, and well defined inward-projecting collars; tops of tubes overgrown by microbial growths; scattered ooids and peloids in micrite of matrix and tube infillings; $\times 10$. D, GSC hypotype No. 115528; S-P Locality No. 10-X (GSC No. O-105757) (lateral equivalent of 10-1A); horizontal section of mature relatively scattered tubes with sub-circular cross section; $\times 14$.



TEXT-FIG. 11. For caption see opposite.

with scattered tubes toward the tops of these mounds (Text-figs 4D, 10). Microbial remains within the 'pillow' structures are discrete to nebulous; they occur as thin overgrowths on clumps of *Tymbochoos* or on a thin layer of sediment that covers the clumps (Text-fig. 11C), as patches between tube clumps and between tubes within the same clump and, more rarely, as faint growths within the tubes. The fact that microbial growths are associated only with relatively poor tube development indicates that the conditions that caused the demise of *Tymbochoos* were advantageous for microbial growth. In some cases, the spread of microbes may have sped up the demise of *Tymbochoos* or even finished them off. However, the fact that most tubes in both environments have some sediment fill and show little evidence of microbial growths, either within the cavity or across the aperture, implies that the microbes generally grew over the tubes after the worms had died and sediment had filtered into the tubes. Stromatolitic growth, which flourished when *Tymbochoos* declined (Text-figs 9A–C, 10), gave structural strength in the absence of a framework structure to both the upper part of the dune-shaped mounds and to the 'pillows'. Penecontemporaneous cementation, which could have been a direct result of high salinity (see below) (e.g. Brantley *et al.* 1984), may have helped to stabilize some of the Braeside 'pillows', as implied by rare surface borings (Text-fig. 7C).

HABITATS

Near-shore settings

The *Tymbochoos* build-ups all developed in near-shore settings. Most of the mounds at both L'Orignal and Dunrobin occur on a packstone-grainstone of ooids, intraclasts and ostracod fragments (Text-fig. 3); these sediments were laid down in tidal channels within tidal flats that were colonized, at least in part, by stromatolites (Steele-Petrovich 1984). In some cases *T. sinclairi* tubes grew on firm stromatolite mounds, some of which were overturned and had probably been undermined by the meandering channel and fallen into it. In other cases dispersed clumps, that developed repeatedly on the hard laminar surfaces of stromatolites, were overgrown by stromatolitic laminae after only a few millimetres of vertical tube growth (Text-fig. 9A); these stromatolites, which occurred at the edge of the environment necessary for *Tymbochoos* survival, probably developed on levee backslopes and in subtidal ponds within the tidal flats. The *Tymbochoos* 'pillow' structures at Braeside developed in a slightly deeper environment, also on an oolite; they are preserved in a packstone-grainstone of ooids, intraclasts, peloids and fossil fragments, which formed discontinuous shoals where relatively gentle waves made contact with the bottom (Steele-Petrovich 1984). The tidal channels and the near-shore shoals where *Tymbochoos* lived were comparatively high-energy settings for this study area, although the oolites, at least in the western part of the valley, formed in muddy environments close to the low-energy limit of ooid formation. Mounds from the lowest stratigraphical occurrence at Dunrobin (Text-fig. 3) are anomalous in not having developed in association with an oolite; they formed in a peritidal environment, probably close the low-tide mark and are preserved in a unit that is sandwiched between intertidal stromatolites. Most Recent serpulid build-ups also occur in near-shore environments, commonly in association with oolites (e.g. Andrews 1964; ten Hove 1979; Bone and Wass 1990; ten Hove and van den Hurk 1993).

Environmental conditions

Mass deaths of young adults after only a short period of tube growth imply fluctuating conditions that for short periods of time were tolerable for both the larvae and young adults and then quickly deteriorated to a state that killed the adults. Only those worms that formed dense frameworks appear to have lived a full life. The dispersed clumps of short tubes throughout the 'pillows' suggest that the 'pillows' were subjected to more marginal, although more uniform, conditions throughout their development than the dune-shaped mounds. The development of dune-shaped mounds at L'Orignal and 'pillows' at Braeside is in keeping with stronger currents in the tidal channels at L'Orignal compared with a quiet and more restricted shallow subtidal setting at Braeside.

There is no evidence that deteriorating conditions toward the tops of the dune-shaped mounds

resulted from changes in either sedimentation rate or current regimes, and the close association of *T. sinclairi* with oolites, which form in shallow agitated conditions, is evidence against suboxia. An alternative explanation is fluctuating salinity: abundant linked evidence on the faunas and the lithofacies within the graben, west of Ottawa, shows that salinity of the near-shore environments fluctuated from hypersaline much of the time, with gypsum forming occasionally, to normal marine more rarely. In comparison, Recent serpulids with the highest salinity tolerance cannot survive salinities above about 55‰ (ten Hove and van den Hurk 1993), while gypsum forms at salinities of at least 125‰ (Brantley *et al.* 1984). Studies of the Ottawa basin in the eastern part of the valley are not sufficiently advanced to determine if hypersalinity was common there also; more sustained and denser tube growth, a lack of gypsum, and more open-marine conditions are in keeping with a lower salinity than in the graben, although the scarcity of near-shore epifaunas in the east may reflect some hypersalinity. The common disruption of microbial textures by burrowing (Text-fig. 9D) indicates that the conditions that adversely affected *Tymbochoos* within the dune-shaped mounds and encouraged microbial growth also sustained burrowers. As burrowers and cyanobacteria can tolerate higher salinities than most epifauna (e.g. Fogg 1973; Savrda *et al.* 1984), their survival in the eastern part of the valley when *T. sinclairi* died fits the explanation that a salinity increase terminated the growth of the dune-shaped mounds. Smaller and sparser clumps of *Tymbochoos* tubes with large microbial growths (Text-figs 4D, 10) are somewhat reminiscent of build-ups in Baffin Bay, Texas, in which mats of green algae have overgrown serpulid reefs that have died since the turn of the century, apparently in response to high salinity (cf. Andrews 1964).

ASSOCIATED FAUNA/FLORA

A diverse and abundant fauna lives in association with tube build-ups today (Woodin 1978). In contrast, only a few species are preserved with the *Tymbochoos* build-ups. Intertube forms were limited to burrowers and to microbial overgrowths that spread as environmental conditions deteriorated and *Tymbochoos* died. A semi-infaunal byssally attached bivalve, *Cyrtodonta breviscula/subcarinata* (*C. breviscula* is the juvenile form of *C. subcarinata*), and a low-spined gastropod, *Raphistomina distincta*, were common to abundant in the tidal channels amongst the asymmetrical dune-shaped mounds; small michelinocerid cephalopods were rare. Ostracods probably lived in tidal pools but not in the channels. *C. breviscula/subcarinata* also lived commonly amongst the *T. sinclairi* 'pillows'; the absence of gastropods from amongst the 'pillows' may be related to weaker microbial growth in that setting.

There is little fossil evidence of possible competition and predation that could have restricted *Tymbochoos sinclairi* to the nearshore region. Because of the morphological and ecological similarities between *T. sinclairi* and Recent serpulids, the two groups would be likely to share the same competitors and predators. Most competitors (barnacles, brown algae) and, except for gastropods, most predators (echinoids, starfish, crabs, fish) of Recent serpulids (Straughan 1969, 1972; Bosence 1973, 1979; O'Donnell 1984) have poor fossilization potentials, and within these groups, only the starfish and gastropods were significant predators during the mid Ordovician. Although there is no evidence for external digestion in Ordovician starfish (Spencer and Wright 1966), the chance of such evidence being preserved is slight, and it is impossible to ascertain the ability of Ordovician starfish to feed on tubicolous forms that could withdraw into tubes. The absence of boreholes in *T. sinclairi* tubes indicates a lack of gastropod predation. Therefore, the effects of competition and predation on the distribution of *T. sinclairi* during the Ordovician appear to have been minor compared with similar effects on serpulids today.

FUNCTIONAL MORPHOLOGY AND SYSTEMATIC AFFINITY

Tymbochoos was neither a serpulid worm (H. A. ten Hove, pers. comm. 1996) nor a vermetid gastropod, each of which belongs to a common Recent group that produces build-ups of calcareous tubes. *T. sinclairi*, with episodic constrictions of the aperture and irregularly spaced constrictions

with anteriorly directed inner collars on the inner tube surface, could not have withdrawn quickly in the face of danger (ten Hove, pers. comm.); in contrast, Recent serpulids, with smooth inner surfaces and constant tube diameters, pull in rapidly. Also, fast expansion to mature diameter of the *T. sinclairi* tube is unlike the gradual and continuing tube expansion of Recent serpulids (H. A. ten Hove, pers. comm.). *T. sinclairi* lacks the coiled protoconch and the complete septa of vermetid gastropods; the inner rings of *T. sinclairi*, although superficially resembling incomplete septa of the vermetids, formed when the whole leading edge of the tube turned inwards, in contrast to the development of vermetid septa from the inner shell layer (cf. Burchette and Riding 1977).

T. sinclairi was a suspension feeder, as indicated by its current-controlled structures, the feeding positions of its tubes, and the living habits of morphologically similar Recent forms. Of tube builders, only the polychaetes have the repetitious segmentation that the semi-regular constrictions and collars on the inner tube wall could reflect. A primitive polychaete, with parapodia and setae on each segment (cf. Fauchald 1975), could have maintained itself at a desired level within the tube by bracing its setae against the irregularities of the inner tube wall. Internal collars may have developed where there was a need for a firmer grip. The inability to withdraw quickly probably reflects the low predation pressures of the Ordovician (see above); as these pressures increased in intensity later in the Phanerozoic (cf. Vermeij 1977), tubicolous animals evolved characteristics that permitted more efficient escape. Analogies with Recent tubicolous suspension-feeding polychaetes indicate that *T. sinclairi* had either a tentacular feeding crown or a system of relatively independent tentacles. Although a feeding crown in the Ordovician would probably have been smaller and not as efficient or as well co-ordinated as in Recent worms, it would have had greater difficulty moving in and out past the anteriorly projecting collars than would independent tentacles. Also, the lack of regular spacing between the long, parallel tubes (see above) argues against feeding crowns. Therefore, *T. sinclairi* probably resided within its tube and fed with a series of short independent tentacles that projected into the water column.

The closest living analogues of *Tymbochoos* appear to be cirratulids. One of these, *Dodecaceria fewkesi*, forms reefs 0.5–1.0 m across, has smooth calcareous tubes without constrictions or inner collars, and each worm feeds with 11 pairs of independent tentacular cirri that project from the tube opening (Meinkoth 1981, p. 433; ten Hove and van den Hurk 1993). A closely related species, *D. coralli* (illustrated by Meinkoth 1981, p. 433), has a generalized polychaete body with setae on each segment and with eight pairs of tentacular cirri near the anterior end. These analogies reflect characteristics of a primitive polychaete and do not necessarily imply a close genetic relationship between the two groups.

Preliminary microscopic examination of the tubes (magnification 250×) consistently shows a single tube layer with a fine radial calcite structure. Studies of the microstructure, which are beyond the scope of this paper and planned for the future, are needed before the systematics of *Tymbochoos sinclairi* can be worked out.

COMMUNITY STRUCTURES OF THE TUBE-SUPPORTING BUILD-UPS DURING THE PHANEROZOIC

Large and consistent differences occur between the community structures of the build-ups of Recent serpulids or vermetids and *T. sinclairi*. Recent tubicolous build-ups serve as refuges for other organisms (Woodin 1978); abundances and diversities of associated organisms are considerably greater within the build-up than away from it. Epifauna associated with Recent serpulid build-ups include stromatolites and other microbial deposits, encrusting bryozoans, byssate bivalves, grazing gastropods and, less commonly, boring sponges and endolithic algae, as well as predatory echinoids, starfish, crabs and fish (cf. Mastrangelo and Passeri 1975; Bosence 1979; Haines and Mauer 1980a, 1980b; Kirkwood and Burton 1988; Rasmussen *et al.* 1993; ten Hove and van den Hurk 1993). Of the 54 infaunal invertebrate species living amongst the serpulid tubes in Delaware Bay, the most abundant are soft-bodied suspension feeders and deposit feeders that burrow into the intertube sediment, build their own tubes and/or inhabit empty serpulid tubes (Haines and Mauer 1980b).

There is little information on the community structures of tubicolous worm build-ups in either the Cenozoic or the Mesozoic. Diversity was high in both a serpulid build-up and a vermetid-algal reef of Miocene age (Pisera 1985; Friebe 1994). Low diversities in the only known Jurassic serpulid structures that are *in situ* (Johnson and McKerrow 1995) could reflect either the evolved complexity of tube communities of that age or the high-stress environmental conditions under which they had developed. However, a low-diversity epifauna, mainly of brachiopods, that was associated with serpulid build-ups that formed below storm-wave base in sediments near the Triassic-Jurassic boundary (Braga and Lopez-Lopez 1989) must represent the true development of intertube diversity associated with build-ups of calcareous tubes at that time.

Faunal diversities and abundances associated with the Ordovician build-ups of *Tymbochoos sinclairi* are very low. Although these build-ups developed in environments that were affected by adverse conditions, there is no difference between the flora/fauna associated with the long, densely packed tubes representing optimal growth and those associated with poorer growth. The presence of gastropods and byssally attached bivalves in the surrounding sediments indicates that conditions were satisfactory, at least at times, for other fauna. Therefore, this low-diversity fossil community probably represents the true complexity of mid Ordovician communities that are associated with calcareous tube-building organisms, and indicates that tubicolous build-ups had scarcely been exploited as a refuge during the mid Ordovician. In particular, relatively constant burrow diameters suggest that the diversity of intertube burrowers was low; there was no encrusting growth on the worm tubes, in spite of the presence of encrusting bryozoans in other mid Ordovician settings; no organisms had bored into the tubes, although the boring of shells occurred elsewhere at this time; byssate bivalves, although associated with the build-ups, did not live amongst the tubes, as they do amongst Recent tubes. Other Palaeozoic tube-dominated build-ups, such as the Cambrian *Scolithus* build-ups (Goodwin and Anderson 1974) and the Carboniferous vermetid build-ups (cf. Burchette and Riding 1977; Wright and Wright 1981), show the same pattern of associated low-diversity communities.

Because build-ups that were formed by different kinds of tube-forming organisms throughout the Phanerozoic occupied many of the same environments, the exploitation of intertube space probably intensified in the different kinds of structures at about the same time. The scanty fossil record suggests that a significant increase in faunal diversities and abundances associated with tube build-ups occurred between the Jurassic and the Miocene. Considering the enormous overall increase in invertebrate diversity at the end of the Cretaceous (e.g. Sepkoski *et al.* 1981), it is reasonable to suggest that the extensive exploitation of intertube space began at that time.

SUMMARY

1. Build-ups of calcareous tubes, previously unknown in rocks older than Devonian, occur in mid Ordovician carbonates of the Ottawa Valley, Canada.
2. The tubes of *Tymbochoos sinclairi* (Okulitch) are circular in cross section and expand quickly to adult diameter (0.95–1.30 mm); irregularly spaced concentric constrictions develop in places into thin anteriorly directed internal collars; growth succeeding the collars began outside and below the collars and subsequently enclosed the collar region.
3. Clumps of tubes formed when the tubes grew sub-horizontally and radially out from small firm attachment areas and then turned and grew vertically.
4. *T. sinclairi* produced dune-shaped structures and smaller isolated pillow-shaped structures.
5. Deteriorating environmental conditions resulted in microbial growths and weak tube development.
6. The build-ups generally formed on oolites, either in intertidal channels or on shallow subtidal shoals.
7. *T. sinclairi* was probably a primitive polychaete that braced itself against the constrictions and collars of the inner tube surface with the setae-bearing parapodia of each segment, and fed with a series of short tentacles that protruded through the tube opening.

8. Predation and competition pressures on *T. sinclairi* were low.

9. Only a few other species lived in association with *T. sinclairi* build-ups, in contrast with the high-diversity communities of refuge-seeking species that live amongst the tubes in Recent calcareous-tube build-ups. The large increase in intertube diversity probably occurred at the end of the Cretaceous.

SYSTEMATIC PALAEONTOLOGY

The figured material is housed in the National Type Collection of Invertebrate and Plant Fossils at the Geological Survey of Canada (GSC), Ottawa.

Genus TYMBOCHOOS gen. nov.

Derivation of name. From the Greek *tymbokōōs* (= mound builder).

Type species. *Tymbochoos sinclairi* (Okulitch, 1937).

Diagnosis. Small calcareous tubes, circular in cross section, expanding quickly from the base to a mature diameter just greater than one millimetre, then growing as straight to slightly sinuous cylinders. Tubes with concentric constrictions, semi-regularly spaced, resulting in corrugated walls. Constrictions extending in places into narrow, anteriorly directed internal collars. Tube growth beyond the collar beginning below the collar on the outside of the tube, and enclosing the collar region. Exterior surface marked rarely by fine longitudinal ridges. Tubes occurring singly or, more typically, in clumps with tubes radiating sub-horizontally from small attachment areas and then growing vertically.

Tymbochoos sinclairi (Okulitch, 1937)

Text-figures 4, 6–11

1937 *Fletcheria sinclairi* Okulitch p. 315, pl. 1, figs 5–7, Text-fig. 1a–c.

1948 *Fletcheria sinclairi* Okulitch; Wilson, p. 43, pl. 21, figs 4–5.

Types. Holotype, Royal Ontario Museum, Toronto, P6871; paratype, ROM P6870; hypotypes, Geological Survey of Canada 115517–115528

Description. Clustered tubes radiating sub-horizontally from small attachment areas and then projecting vertically (Text-figs 4B, 8A, 9A–B, 11A, C). Tubes circular in cross section (Text-figs 8B, 11B, D) with diameters increasing quickly from about 0.12 mm to a maximum of 1.50 mm (usually 0.95–1.30 mm); subsequent tube growth as straight to slightly sinuous cylinders (Text-figs 4B–C, 8A, 9A–B, 11A, C). Wall thickness varying greatly, probably due to diagenesis. Semi-regularly spaced concentric constrictions common and resulting in corrugated inner and outer walls (Text-figs 4C, 8A, 9A–B, 11A, C). In places these constrictions developing into thin, anteriorly directed, internal collars that result from inward growth of the leading edge of the shell; succeeding growth beginning on the outside of the tube below the collar and subsequently enclosing the collar region (Text-fig. 11C). Exterior sculpturing varying: most tubes unridged, but about 20 fine longitudinal ridges occurring on others (Text-figs 4C, 11B). Growth forms including (1) dense concentrations of clumps with densely packed vertical to sub-vertical tubes (up to 0.4 m long) (Text-figs 4B, 8A), occurring only in dune-shaped structures (Text-fig. 4A, 6); (2) sparser concentrations of clumps with loosely packed vertical to sub-vertical tubes (a few mm long) (Text-figs 9A–B, 10–11), occurring in isolated pillow-shaped structures (Text-fig. 7); (3) isolated tube clumps on certain bedding planes.

Remarks. Okulitch (1937) related this species to the Chazyan tabulate coral *Fletcheria* [*Eofletcheria*] *incerta* (Billings) from the mid Ordovician (Chazyan) Mingan Formation of the Mingan Islands, Quebec, and assigned it to a new species, *Fletcheria sinclairi*, on the basis of different tube growth, smaller tube diameter, lack of septa and tabulae, a markedly rugose exterior, and rejuvenescence (i.e. a new start after growth of a collar). Bassler (1950, p. 266) noted similar

corrugated walls in the tubicolous annelids *Conchiolites* and *Cornulites*. The present study confirms that this species is not a coral, but a calcareous tube, probably of a primitive polychaete. It is here assigned to a new genus *Tymbochoos*.

Occurrence. G. W. Sinclair (pers. comm. 1970) collected the type specimens from the Pembroke Quarry (Text-fig. 1) (see Goudge 1938, p. 162). Kay (1942) reported 4.3 m of Lowville Beds in this quarry. According to C. R. Barnes (pers. comm. 1995), the quarry in 1966 contained 2.0 m of Pamela Beds overlain by 4.2 m of Lowville beds. In 1970, B. A. Liberty and T. E. Bolton noted this species in the upper exposed Lowville beds of the quarry. Previous publications report *F. sinclairi* from probable late Chazy rocks in the vicinity of Pembroke (Okulitch 1937; Bassler 1950, p. 266), the Pamela Beds near Ottawa (Okulitch 1937) and the Pamela Beds on Highway 17 about 10 km south of Pembroke (Wilson 1948). Specimens studied here are from the Pamela Beds near L'Orignal and Dunrobin and Lowville Beds at Braeside (Text-fig. 2).

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