CHAPTER 7

U-SHAPED BURROWS

U-SHAPED BURROWS

7.1. INTRODUCTION

U-shaped burrows can be divided into the following four categories.

1. Spreite-bearing vertical U-tubes (e.g. Diplocraterion).
2. Spreite-bearing bedding-parallel or slightly oblique U-tubes (e.g. Rhizocorallium).
3. Spreite-free vertical U-tubes (e.g. *Arenicolites*).
4. Spreite-free horizontal U-tubes (presently unnamed).

Burrows belonging to all except the forth category occur in the present study area, the examples of categories two and three being particularly diverse (as is commonly the case elsewhere in the world) and category three being represented by a single ichnogenus. The following sections in the this chapter discuss burrows in each of the first three categories in some detail.

7.2. SPREITE-BEARING VERTICAL U-SHAPED BURROWS (DIPLOCRATERIIDS)

7.2.1. Definition and terminology

U-shaped domichnia or dwelling-tubes provide less permanent or semi-permanent domiciles for hemisessile, commonly suspension-feeding organisms. They are simple U-shaped structures perpendicular or steeply-inclined at various angles to the bedding planes. They are a full-relief and endogenic type of structure (Seilacher, 1964a; Webby, 1969; Martinsson, 1965, & *1970;* & Chamberlain, 1971).

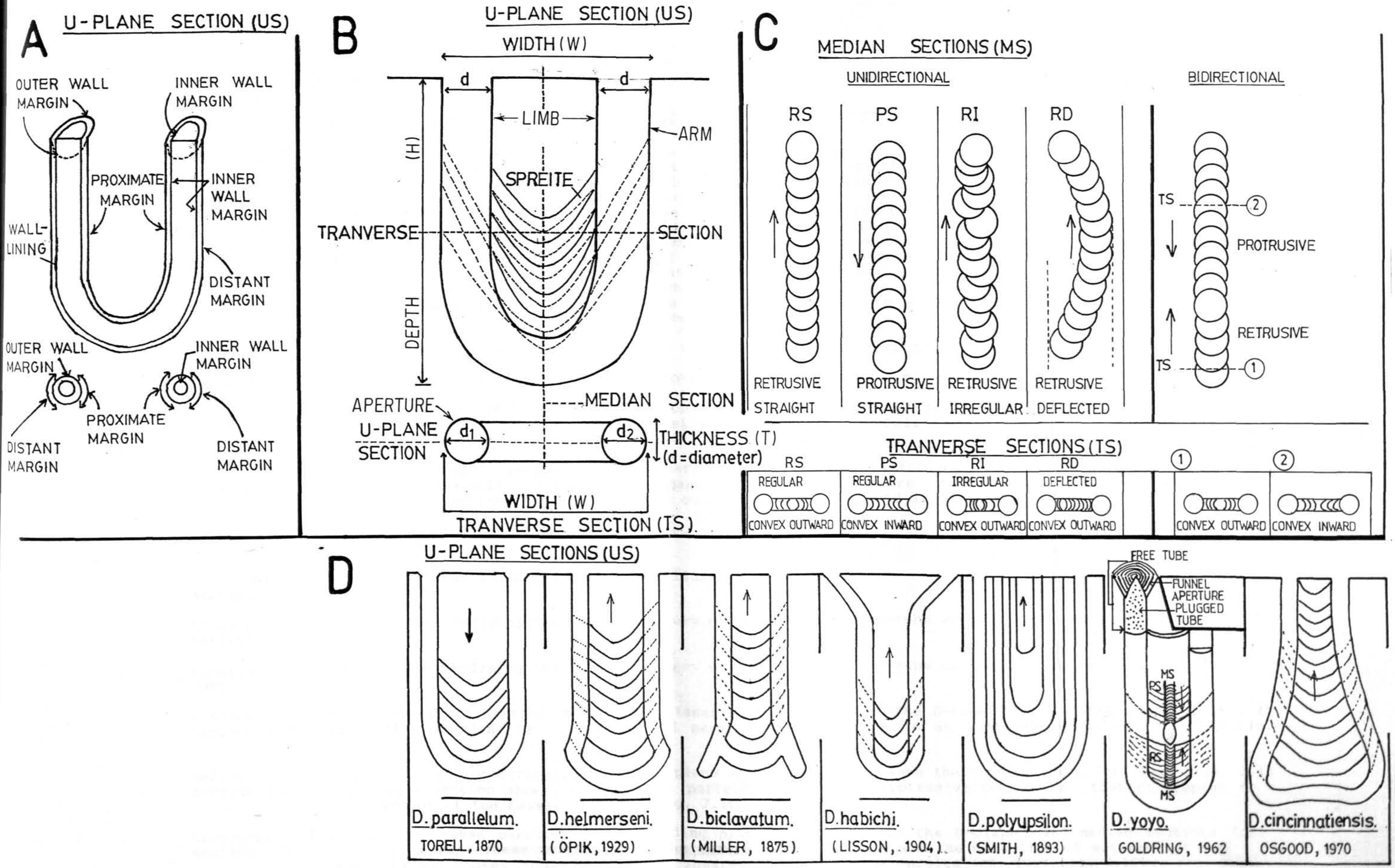
U-shaped dwelling-burrows that are normal to or steeply-inclined to bedding are probably the predominant variety of

TEXT-FIG. 7.1. Definition diagram of vertical spreite-bearing U-shaped burrows of Diplocraterion (Torell, 1870) and its various species. See also Table 7.1 for definition of terminology.

A & B. Definition of morphological terms and dimensional parameters as seen in the U-plane and transverse sections.

C. Definition of the various patterns of spreite development as seen in median (top) and transverse (bottom) sections. Note distinction between protrusive and retrusive patterns.

D. Definition of the various species of Diplocraterion (Torell, 1870) as seen in the U-plane section with the qualification that the figure depicting D. yoyo is in part three dimensional. Diagram involves a revision in the case of D. polyupsilon (cf. Text-Fig. 7.2).


A
U-PLANE SECTION (US)
OUTER WALL MARGIN
INNER WALL MARGIN
PROXIMATE MARGIN
INNER WALL MARGIN
WALL-LINING
DISTANT MARGIN
OUTER WALL MARGIN
INNER WALL MARGIN
PROXIMATE MARGIN
DISTANT MARGIN
DISTANT MARGIN
B
U-PLANE SECTION (US)
WIDTH (W)
d
d
LIMB
ARM
(H)
SPREITE
TRANVERSE SECTION
DEPTH
MEDIAN SECTION
APERTURE
U-PLANE SECTION
d1
d2
THICKNESS (T)
(d=diameter)
WIDTH (W)
TRANVERSE SECTION (TS).
C
MEDIAN SECTIONS (MS)
UNIDIRECTIONAL
BIDIRECTIONAL
RS
PS
RI
RD
RETRUSIVE STRAIGHT
PROTRUSIVE STRAIGHT
RETRUSIVE IRREGULAR
RETRUSIVE DEFLECTED
TS
PROTRUSIVE
RETRUSIVE
TS
TRANVERSE SECTIONS (TS)
RS
PS
RI
RD
REGULAR
REGULAR
IRREGULAR
DEFLECTED
CONVEX OUTWARD
CONVEX INWARD
CONVEX OUTWARD
CONVEX OUTWARD
CONVEX OUTWARD
CONVEX INWARD
D
U-PLANE SECTIONS (US)
FREE TUBE
FUNNEL APERTURE
PLUGGED TUBE
MS
PS
RS
MS
D. parallelum. TORELL, 1870
D. helmerseni. (ÖPIK, 1929)
D. biclavatum. (MILLER, 1875)
D. habichi. (LISSON, 1904)
D. polyupsilon. (SMITH, 1893)
D. yoyo. GOLDRING, 1962
D. cincinnatiensis. OSGOOD, 1970

TEXT-FIG. 7.1

TABLE 7.1. Glossory of terms (emended in some cases) and parameters used in the description of vertical spreite-bearing U-shaped dwelling-burrows.

Arm:	The cylindrical vertical portions of the U-tube.
Aperture:	The opening of each arm of the U-tube at the depositional interface; the aperture can have different shapes, sizes, and inclination: e.g., straight, vertical, inclined, small, large and funnel-shaped. Inasmuch as the top part of the U-shaped burrows is erosionally removed either penecontemporaneously with burrow excavation or in Recent times in the rock exposures containing the burrows, it is difficult to resolve in the absence of a distinctive morphology at the top of U-tube (e.g., such as a funnel-shaped opening or a symmetrically divergent pattern of the top of the U) whether or not the original opening of the tube at the sediment surface is preserved. In the absence of distinctive morphologies such as those mentioned above the vent of each arm of the U-tube is characteristically a simple vertical cylinder and raises the possibility that it represents a formerly lower part of the arm that has been brought closer to the sediment/outcrop surface through erosional loss of the original aperture. In this report such simple vertical cylindrical vents are generally referred to as openings and the morphologically distinctive vents are referred to as apertures.
Free tube:	The portion of the arm as measured from the aperture to the first spreiten.
Plugged tube:	That part of the free tube that lies above the topmost retrusive spreiten (cf. Plate 36 Figs. a & b).
Limb:	The strip of spreite between the two openings of the U-tube. As so defined this term applies only to protrusive spreite since retrusive spreite extend across the full width of the burrow to the distant margins.
Wall/wall-lining:	''Raumauskleidung'' (Reineck, 1957; Schafer, 1962, p.331, & p.427); one or more layers of mud or coarser sediment, originally pervaded by organic mucus, that is/are plastered onto the margin of the burrow to strengthen it and prevent its collapse; commonly found in all domichnia burrows.
Outer wall margin:	Outer peripheral interface of the U-tube.
Inner wall margin:	Inner peripheral interface of the wall-lining.
Distant margin:	The interface defining the outer periphery of the arms of the U-tube as seen in U-plane section.
Proximate margin:	The interface defining the inner periphery of the arms of the U-tube as seen in U-plane section.
U-plane section (US):	A most important section which is coplanar with the plane of the U-tube (cf. Text-Figs. 2.1A & 1B). It shows the U-outline of the burrow and permits classification to an ichnogeneric level (cf. Text-Fig. 7.1D).
Median section (MS):	A vertical section orthogonal to the U-plane section midway between the arms of the U (cf. Text-Figs. 2.1B & C). This section shows the different patterns of spreite (protrusive/retrusive) that correspond to the movement of the animal (cf. Text-Fig. 7.1C).
Tranverse section (TS):	Any section taken parallel to the bedding plane, and normal to the U-plane and median sections (cf. Text-Fig. 7.1C). These sections show the nature of the spreite and the direction of movement of the animal by the convex-outwards or convex-inwards polarity of the spreite (cf. Text-Fig. 7.1C).

Table 7.1. (continued)

Width (W):	The distance between the distant margins (Text-Fig. 7.1B). Also called ``length'' by some workers.
Depth (H):	Vertical length of the U-shaped structures.
Thickness (T):	The distance between the two planes that are parallel to the U-plane and that wholly contain both the U-tube and its spreite (Text-Fig. 7.1B); also called ``breadth'' by some workers. In tranverse sections cut through the spreite-free arms of the U-tube and in tranverse sections cut through the spreite-bearing lower part of the U-tube and in which the spreite are neither deflected nor irregular (cf. Text-Fig. 7.1C) this distance will equal the diameter of the U-tube. This parameter commonly increases with increasing depth.
Diameter (d):	Diameter of the aperture/opening of the U-tube. It is also equivalent to the thickness/breadth of the burrow in tranverse sections cut through the free arms (cf. Text-Fig. 7.1B).
Spreite (pl) Spreiten (s) (Gr.) Septum (Lat.) Traverse (Fr.):	Arcuate relics/traces of the excavation in U-tube burrows; can be formed variously: (a) as a consequence of movement during deposit-feeding; (b) as a consequence of the growth of the inhabitant; (c) as a result of permeability contrasts in different layers of the sediment; and (d) movements of the inhabitant organism in response to sedimentation and/or erosion. In the U-plane section spreite forms a series of arcuate layers that bridge across the arms of the U and which are generally parallel to the base of the U-shaped burrow. The following significant characteristics define the nature of spreite.
Protrusive spreite (PS):	A series of arcuate layers of sediment that indicate a history of progressive deepening of the burrow, possibly as a consequence of sedimentation. As viewed in median section (cf. Text-Fig. 7.1C), the thickness of the spreite may increase with depth and the cresent-shaped envelopes that define each individual spreiten are invariably convex upward. As viewed in tranverse sections (cf. Text-Fig. 7.1C), these envelopes are also crescent-shaped and are convex inwards. As seen in U-plane section, (cf. Text-Figs. 7.1B & 1D), these envelopes are also crescent-shaped, are invariably convex downwards regardless of whether the spreite are protrusive or retrusive, and, unlike the retrusive spreite which extend across the full width of the burrow to the distant margins, extend only between the porximate margins (cf. Text-Fig. 7.1B).
Retrusive spreite (RS):	A series of arcuate layers of sediment that indicate a history of progressive elevation of the bottom of the U-tube possibly in reponse to erosion of the substrate. As viewed in median section (cf. Text-Fig. 7.1C), the envelopes of the individual spreiten are crescent-shaped and are invariably convex downwards. As viewed in tranverse sections (cf. Text-Fig. 7.1C), these envelopes are also crescent-shaped and are convex outwards. As seen in U-plane section (cf. Text-Figs. 7.1B & D), the arcs extend to the distant margins of the U (indicated by the dashed lines in Text-Fig. 7.1B).
Continuous spreite:	Arcuate layers of spreite (either protrusive or retrusive or both) that are developed continuously between the two arms of a U (i.e., without loss of lateral definition).
Discontinuous spreite:	Arcuate layers of spreite (either protrusive or retrusive or both) that are developed discontinuously between the two arms of the U (i.e., with loss of lateral definition).
Regular spreite:	Arcuate layers of spreite characterised by even and regular spacing.
Irregular spreite:	Arcuate layers of spreite characterised by uneven or irregular spacing.
Deflected spreite:	Spreite formation either in regular or irregular curvilinear pattern beyond the U-plane (cf. Text-Fig. 7.1C).

Table 7.1. (continued)

Unidirectional spreite:	Spreite formation in one direction (cf. Text-Fig. 7.1C) indicating a history of unidirectional movement of the producer organism, either downwards or upwards.
Bidirectional spreite:	Spreite formation in two directions (cf. Text-Figs. 7.1B & C) indicating a history of reversal of animal movement, either just once or recurrently (cf. Goldring, 1962, text-fig. 3).
Distance-to-nearest-neighbour (DNN):	The distance between two nearest neighbours of U-tube burrows (Text-Fig. 7.6). The measurement can be made in several different ways (cf. Text-Fig. 7.6). In Text-Fig. 7.6 the distances labelled A,C,D, and E in the various diagrams are the measured distances between the two adjacent and diagonally opposed apertures of the burrows of deposit-feeding organisms, and the distance B is the measured distance between the two midpoints of each burrow limb (defined as the point that is equidistant from the paired openings or apertures of each burrow of suspension-feeding organisms). For comparative population density purposes it is also important to measure the overall surface area of the bedding plane bearing the U-shaped burrows (Table 7.8).

dwelling-burrow in many environments from Cambrian to Recent. Most of them have spreite in a "traverse zone" (also called "disturbed zone") between the limbs or arms of the **U** (Text-Fig.2.1). These spreite-bearing tubes have been studied and described by various authors commencing more than a century ago (Torell, 1870; Smith, 1893; Lisson, 1904; Opik, 1929; Howell, 1957; Goldring, 1962; Osgood, 1970; Knox, 1973; and Fürsich, 1974). However, there is still some inconsistency in the terminology, description and taxonomic position of these vertical spreite-bearing U-tubes and it is therefore necessary to clarify the meaning of certain terms before their further use. The meaning of most of the terms used here is clarified in Table 7.1 and Text-Figure 7.1.

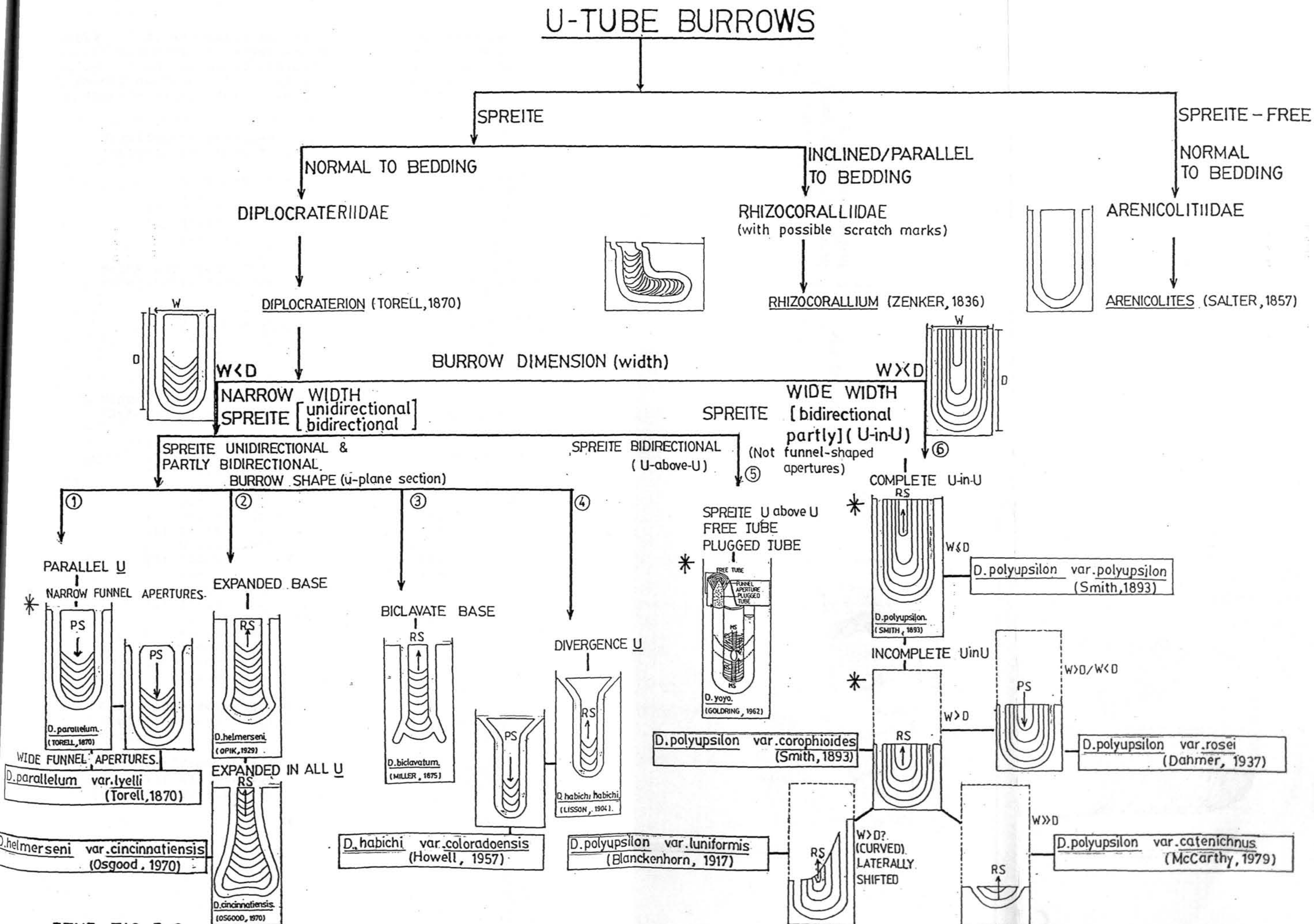
7.2.2. Proposed new classification of vertical spreite-bearing U-shaped burrows

Two ichnogenera fall within this group of vertical spreite-bearing U-shaped burrows, namely Diplocraterion and Polyupsilon (Corophioides). From the diagnoses of these two ichnogenera (Table 7.2) it becomes apparent that there are no basic differences between them at the ichnogeneric level. The difference between Diplocraterion (Torell, 1870) and Polyupsilon (Howell, 1957) that are evident can be regarded as of ichnospecific rather than ichnogeneric significance, and for which reason the ichnotaxonomic status of Polyupsilon (Howell, 1957) is revised to that of a species of Diplocraterion. The two major significant differences between them are: firstly, the contrasting patterns of spreite as seen in the U-plane (i.e., U-in-U

TABLE 7.2. General diagnoses of all ichnogenera characterised by vertical spreite-bearing U-shaped structure.

<u>Diplocraterion</u> Torell, 1870.	U-shaped burrow with spreite, invariably perpendicular to the bedding plane; funnel-shaped apertures (Häntzschel, 1962, p.W192, and 1965, p. 32).
<u>Polyupsilon</u> Howell, 1957.	U-shaped burrow with retrograde (i.e., retrusive) spreite (Howell, 1957; Häntzschel, 1966, p. 15).
<u>Corophioides</u> Smith, 1893 (in Knox, 1973).	Vertical spreite-bearing U-shaped burrows in which the upper parts of both tubes show a progressive lateral displacement in the same direction within the plane of the U associated exclusively with retrusive spreite, thus manifesting an oblique upward movement of the U-tube with time.

TEXT-FIG. 7.2. Proposed classification of U-shaped burrows with emphasis on vertical spreite-bearing burrows of the Family Diplocrateriidae. The new classification is necessary because it is important to eliminate a large number of ill-defined U-shaped burrows and synonyms from the previous literature to minimise difficulties involved in assigning ichnogenera and species. The morphological criteria etc. on which the classification is based are detailed in Table 7.3 and the original and revised ichnotaxonomic names are given in Table 7.4. The classification differentiates the Diplocrateriidae at ichnogeneric, ichnospecific and variety levels. Asterisks indicate burrow forms that are present in the study area.


U-TUBE BURROWS
SPREITE
SPREITE – FREE
NORMAL TO BEDDING
INCLINED/PARALLEL TO BEDDING
NORMAL TO BEDDING
DIPLOCRATERIIDAE
RHIZOCORALLIIDAE (with possible scratch marks)
ARENICOLITIIDAE
DIPLOCRATERION (TORELL, 1870)
RHIZOCORALLIUM (ZENKER, 1836)
ARENICOLITES (SALTER, 1857)
W
D
BURROW DIMENSION (width)
W<D
W>D
NARROW WIDTH
SPREITE [unidirectional bidirectional]
WIDE WIDTH
SPREITE [bidirectional partly] (U-in-U)
(Not funnel-shaped apertures)
SPREITE UNIDIRECTIONAL & PARTLY BIDIRECTIONAL
BURROW SHAPE (u-plane section)
SPREITE BIDIRECTIONAL (U-above-U)
①
②
③
④
⑤
⑥
PARALLEL U
NARROW FUNNEL APERTURES
*
PS
D. parallelum. (TORELL, 1870)
WIDE FUNNEL APERTURES.
D. parallelum var. lyelli (Torell, 1870)
EXPANDED BASE
RS
D. helmerseni (OPIK, 1929)
EXPANDED IN ALL U
D. helmerseni var. cincinnatiensis (Osgood, 1970)
D. cincinnatiensis. (OSGOOD, 1970)
BICLAVATE BASE
D. biclavatum. (MILLER, 1875)
DIVERGENCE U
D. habichi habichi (LISSON, 1904).
D. habichi var. coloradoensis (Howell, 1957)
SPREITE U above U
FREE TUBE
PLUGGED TUBE
FREE TUBE
FUNNEL APERTURE
PLUGGED TUBE
MS
D. yoyo. (GOLDRING, 1962)
D. polyupsilon var. luniformis (Blanckenhorn, 1917)
COMPLETE U-in-U
D. polyupsilon. (SMITH, 1893)
D. polyupsilon var. polyupsilon (Smith, 1893)
INCOMPLETE UinU
W>D/W<D
D. polyupsilon var. corophioides (Smith, 1893)
D. polyupsilon var. rosei (Dahmer, 1937)
W>D? (CURVED) LATERALLY SHIFTED
W>>D
D. polyupsilon var. catenichnus (McCarthy, 1979)

TEXT-FIG. 7.2

TABLE 7.3. Morphological features, dimensional parameters, and other criteria of major and minor genetic (i.e., ethological) value in the proposed classification of vertical spreite-bearing U-shaped burrows (cf. Text-Fig. 7.2). Some additional features of no genetic significance are also included for completeness.

Significant features
(Diagnostic characteristics at the ichnogeneric level)

(1) U-shaped burrow, having two parallel arms with apertures/openings.
(2) Presence of spreite.
(3) Highly discordant (essentially vertical) attitude to bedding.

Major accessory features
(Diagnostic features at the ichnospecific and variety levels)

(1) U-shaped burrow outline in the U-plane section.
(2) U-in-U or U-above-U pattern of spreite.
(3) Major burrow dimensions and dimensional parameters (width, depth, thickness of U-tube, and width/depth ratio).

Minor accessory features
(Diagnostic features at the variety level)

(1) Unidirectional spreite (protrusive or retrusive).
(2) Bidirectional spreite (protrusive and retrusive).
(3) Regularity of spacing of spreite.
(4) Lateral preservation of spreite (continuous or discontinuous).
(5) Deflection of spreite beyond the U-plane.
(6) Oblique (i.e., vertico-lateral) displacement of the U-tube in the vertical plane.
(7) Geometry and size of the apertures (cylindrical-vertical, cylindrical-inclined, funnel-shaped, small/large).
(8) Structure, composition and thickness of the U-tube wall and its outer ornamentation (uni-/multilayered, mud/mucous etc., thin/thick, with/without bioglyphs).
(9) Minor burrow dimensions (i.e., thickness; and diameter of aperture/opening).

Other accessory features
(Modifications regarded here as being without taxonomic value)

(1) Free tube and plugged tube.
(2) Association of faecal pellets either within or outside the burrow.

pattern in Polyupsilon and U-above-U pattern in Diplocraterion; cf. Text-Fig.7.1D); and secondly, the significantly larger width/depth ratio of the Polyupsilon burrows compared to that of the Diplocraterion burrows in cases where the burrows are fully/near-fully preserved (cf. Table 7.3; Text-Figs. 7.4 & 7.5). The ichnogenus Corophioides (Smith, 1893; in Knox, 1973) is actually a synonym of the genus Polyupsilon (Howell, 1957).

These apparent taxonomic differences can be reconciled in a comprehensive revised classification of vertical spreite-bearing U-shaped burrows as explained below.

The necessary prerequisite for the proposed classification (Text-Fig. 7.2) is a review of the ichnotaxonomy of the previously described vertical U-shaped burrows, an ethological analysis of their morphology and a revision of their ichnotaxonomic status on the basis of perceived morphological differences of inferred ethological significance vis a vis morphological artifacts of purely preservational significance. To devise an appropriate and viable classification (cf. Text-Fig.7.2) it is necessary to establish what the significant morphological features are in the higher levels of the classification and similarly the important major and minor accessory morphological features in the lower levels of the classification. The features that underpin the various levels of the proposed classification are detailed in Table 7.3.

7.2.3. Evaluation of the criteria on which the classification is based

Formation of spreite:

The presence of spreite is one of the most significant features in these U-shaped burrows. It is therefore necessary to define how the spreite are formed, why the organism had to make them, and why these become very important issues in the classification. The various patterns of spreite that occur and the ethology that these patterns manifest are major diagnostic criteria in the classification.

Spreite are defined as arcuate relics of excavation by the producer animal. There are several possible explanations of the formation of spreite in a burrow involving both infaunal suspension-feeders and infaunal deposit-feeders (Fürsich, 1974).

Spreite formed through ingestion by infaunal deposit-feeders: Spreite formed by infaunal deposit-feeders in U-shaped burrows are to be expected in burrows which are excavated and mined horizontally in nutrient layers (e.g. Rhizocorallium) from consideration of the mechanics of the burrows' progressive relocation and the problems involved in the storage of the excreted sediment (Schäfer, 1972, and Fürsich, 1974). But this type of spreite formation associated with vertical U-shaped burrows is less explicable where the burrows have been formed by deposit- (as opposed to suspension-) feeders (Richter, 1926; Goldring, 1962; and Seilacher, 1967). This is because the deposit-feeders could be expected to exploit the nutrient-rich sediment parallel to bedding from shallow burial depths rather than from deeper burial depths necessitating more steeply-inclined burrows. Instinctively, one would normally expect that maintenance of the animal's life-support systems would be harder at the greater burial depths.

Spreite formed during growth of the organism in the burrow: That spreite are formed by the enlargement or the growth of the producing organism is indicated by the downward increase in the length and the thickness of the limb of protrusive spreite in some burrows (e.g., Fürsich, 1974b).

Spreite formed as a consequence of textural layering (i.e., lamination/bedding) in the sediments being burrowed: When the organism begins to excavate the U-shaped burrow in fairly cohesive fine-grained sediment, the angle between the arms of the U is initially very large, or in other words the inward inclination of the arms of the U-tube is at a shallow angle. As the burrow gradually deepens the inter-arm angle decreases until the tubes of the U are vertical and open at the surface in order to maintain continuous water circulation during all stages of the burrow's development (Reinick, 1958). A natural consequence of the deepening of the burrow in this way is infilling or back-filling of the excavated region between the arms of the U and above the animal's location at the base of the U. A consequence of the burrow's progressive downward passage through texturally-layered sediment is that the same textural layering will be manifested in the back-filled zone to produce what is called spreite. However, where a burrow is excavated in texturally-uniform sediment (e.g., clay or clean well-sorted sand) such textural layering in the back-filled zone between the arms of the U will normally not occur unless through the introduction in this zone of faecal sediment produced by the animal.

Spreite formed by the upward or downward movement of suspension-feeders in response to sedimentation or erosion: Spreite can be formed due to the upward or downward movement of the suspension-feeding organisms in response respectively to sedimentation (resulting in retrusive spreite) and erosion (resulting in protrusive spreite). This behavior is an expression of the animal's need to keep itself at an optimum distance from the depositional interface (Goldring, 1962). As a suspension-feeder the animal tends to stay in a balanced position - near enough to the sediment surface to get food from the bottom currents, but deep enough to maintain maximum protection.

Morphology and classification of spreite:.

The zone of spreite development forms the volumetrically major part of the U-shaped trace and because its pattern manifests the ethology of the producer organism it therefore constitutes the best available taxonomic criterion for differentiation of the ichnotaxa at the ichnospecies level. In general there are several significant characteristics that define the specific nature of the spreite.

Protrusive or retrusive spreite (unidirectional): The spreite result from the unidirectional shift of the organism: either upward, generating retrusive spreite (in response to bed accretion); or downward, generating protrusive spreite (in response to bed erosion). This vertical migration of the burrow takes place essentially within the U-plane and involves a vertical repetition of the vertex/base of the U (cf. Text-Fig.7.1).

Protrusive and retrusive spreite (bidirectional): In this case the spreite result from alternating upward and downward movements of the organism resulting respectively in retrusive and protrusive spreite (cf. Text-Fig.7.3A).

Regularity/irregularity of spacing of spreite: The development of spreite can involve equal spacing (regular pattern) or unequal spacing (irregular pattern) (cf. Text-Fig.2.3C). Normally the spreite between the two arms of the U-tube are somewhat irregular and the individual spreite are not everywhere parallel, but instead can be crowded or concentrated towards one arm. This irregular pattern of spreite reflects unstable or less stable behavior of the animal and is most likely related to the relative degree of heterogeneity/homogeneity of the sediment (i.e., grain-size contrast/uniformity from bed to bed or lamina to lamina). Indeed, regularity and irregularity of the spreite pattern can both occur in the one specimen; hence it is not an appropriate characteristic to be used at the ichnospecific level of classification.

Degree of lateral definition of the spreite: Spreite can be preserved either in a laterally continuous or discontinuous pattern in the U-tube burrow (Text-Fig.7.3C). The laterally discontinuous spreite probably manifest relatively rapid adjustment in the position of the U-tube in response to rapid erosion or sedimentation. Therefore the degree of lateral definition of the spreite reflects only ethologically minor differences of the same animal's intention to maintain the optimal depth of the burrow. Hence, it is not a very important characteristic and is unsuitable for taxonomic differentiation at the ichnospecific level.

Deflection of spreite: In some cases spreite can be curved or deflected beyond the U-plane of the burrow (Text-Fig.7.1C). Such deflected spreite are best seen in median section (Text-Fig.7.1C) This phenomenon also constitutes a minor irregularity and is not an important feature of ichnotaxonomic value.

Major patterns of spreite: There are two major distinct patterns formed by the spreite. The normal protrusive and/or retrusive type of development in Diplocraterion is a U-above-U pattern (Text-Fig.7.1D) in which the ratio of the vertical-relief-to-limb-width of each spreiten is more or less constant throughout the burrow. The other type of spreite development occurs in Diplocraterion polyupsilon and involves a retrusive U-in-U pattern (Text-Fig.7.1D) in which the ratio of the depth-to-width of individual spreiten decreases progressively from the oldest to the youngest generation (see also Knox, 1973, fig.7). This pattern of retrusive spreite development involved the progressive upwards and inwards concentric contraction of the U-tube within the U-plane suggesting that it manifests sediment-mining activity of a deposit-feeder.

These two contrasting types of spreite were the basis for distinction between D. parallelum and D. polyupsilon (= Corophioides) by Knox (1973). Intermediate and gradational forms between these two types of spreite pattern were subsequently discovered by Knox (in Fürsich, 1974a). Hence, differentiation of these two genera on this basis alone is not justified and it is better to retain the name Diplocraterion (which has priority) for both these forms. Nevertheless, these two contrasting patterns of spreite would appear to manifest a different ethology and it

TEXT-FIG. 7.3.

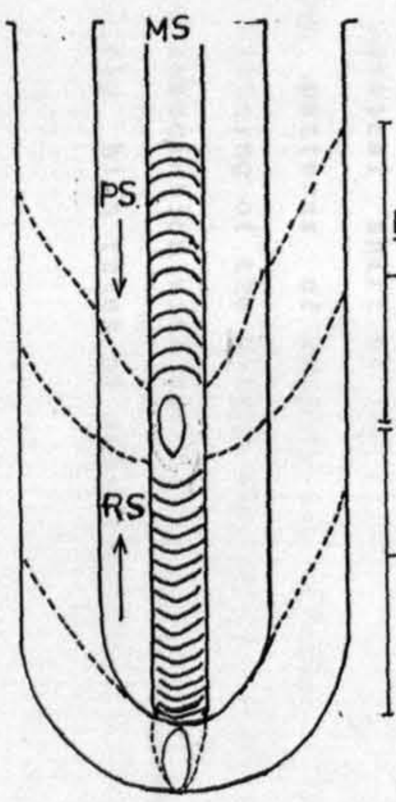
A. Diagram of hypothetical bidirectional spreite-bearing U-tube burrow formed by the movements of an animal as follows: stage 1, protrusive spreite (as in Polyupsilon coloradoensis (Howell, 1957)); stage 2, retrusive spreite (as in Diplocraterion habichi (Lisson, 1904). D. yoyo (Goldring, 1962) is here considered to be an emended ichnogenus with bidirectional spreite.

B. Two similar U-shaped burrows with different directions of spreite: Corophioides luniformis (Blanckenhorn, 1917) with unidirectional retrusive spreite (lower diagram); and C. rosei (Dahmer, 1937) with unidirectional protrusive spreite (upper diagram). Seilacher placed these two forms into the one ichnogenus, C. luniformis (Seilacher, 1963). In the proposed classification they are separated as different varieties which are believed to manifest the animal's movements (behaviour) in response to substrate accretion and degradation respectively. The revised names are in the boxes at right.

C. D. parallelum (Torell, 1870) from the Corallian (Upper Jurassic) of Dorset, southern England, showing both regular and irregular spacing and laterally continuous and discontinuous spreite (Fürsich, 1974a). Both these latter features are not regarded as of ichnogeneric or ichnospecific value in the proposed classification because they are minor accessory features that are believed to have been produced by minor adjustment of the animal in response to substrate accretion and degradation. The revised name is in the box at right.

	PREVIOUS NAMES OF ICHNOGENERA AND THEIR CHARACTERISTICS.	ASSIGNMENT OF SOME PROBLEMATIC ICHNOGENERA IN THE PROPOSED CLASSIFICATION AND THEIR EMENDED CHARACTERISTICS, TOGETHER WITH UNRECORDED FORMS.

A



Polyupsilon coloradoensis (Howell, 1957)

STAGE 1

D. habichi (Lisson, 1904)

STAGE 2

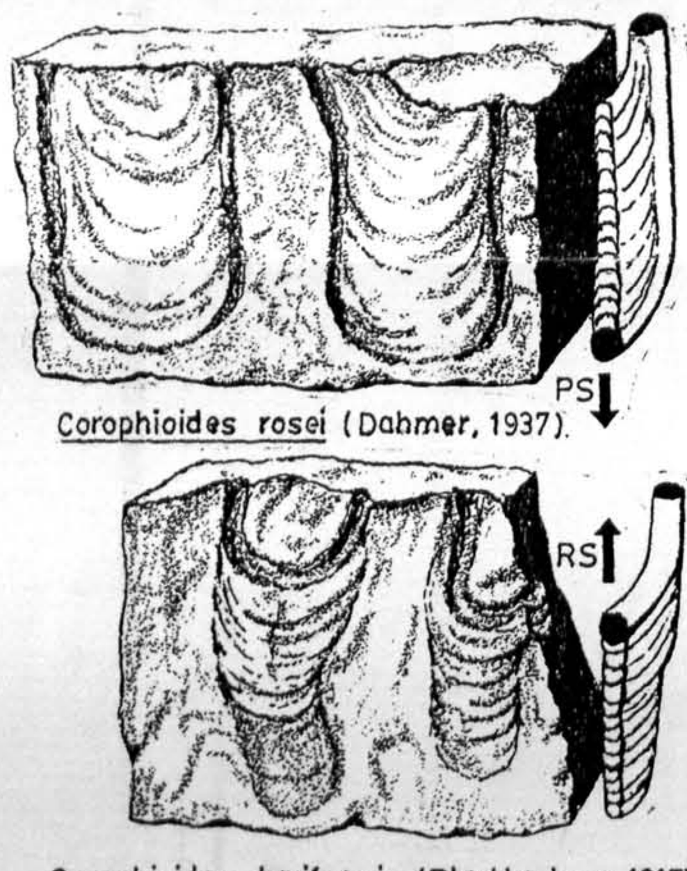
D. yoyo (Goldring, 1962).
Bidirectional spreite
Free and plugged tubes.

D. yoyo (Goldring, 1962).
Bidirection spreite.
Free and plugged tube.

Bidirectional spreite with divergent apertures [unrecorded].

Bidirectional spreite without free and plugged tubes [unrecorded].

B



Corophioides rosei (Dahmer, 1937).

Corophioides luniformis (Blanckenhorn, 1917)

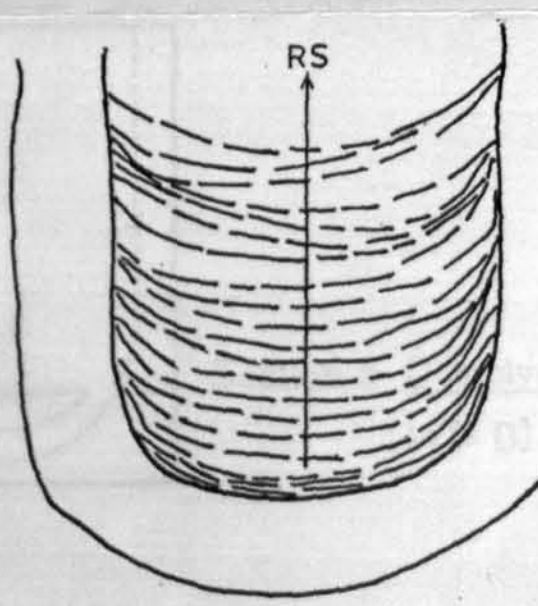
Corophioides rosei (Dahmer, 1937).
Unidirectional protrusive spreite.

Corophioides luniformis (Blanckenhorn, 1917).
Unidirectional retrusive spreite.

Diplocraterion (polyupsilon) rosei (Dahmer, 1937).
W > D. / W < D
Unidirectional protrusive spreite.

Diplocraterion (polyupsilon) luniformis (Blanckenhorn, 1917).
W ? D (U laterally shifted).
Bidirectional spreite (partly).
Unidirectional retrusive spreite (mainly).

C



Corophioides erraticus (Richter, 1926).
STAGE 2 (irregular).

Corophioides luniformis (Blanckenhorn, 1917).
STAGE 1 (regular).

Diplocraterion (polyupsilon) corophioides (Smith, 1893).
Bidirectional spreite (partly).
Unidirectional retrusive spreite (mainly).
Regular and/or irregular spacing of spreite.
Continuous and/or discontinuous occurrence of spreite laterally.

Diplocraterion parallelum (Torell, 1870).
[Corallian (J_3) of Dorset, southern England] (in Fursich, 1974).

TEXT-FIG. 7.3

is therefore desirable to retain this variable for ichnotaxonomic differentiation at the ichnospecific level in the classification (cf. Text-Fig. 7.2, and Table 7.3).

Other accessory features of the burrows:

Burrow outline in the U-plane section: The burrow outline in U-plane section is the most important major accessory feature in the proposed classification (Table 7.3). It is a uniquely distinctive morphological feature that allows the separation of Diplocràterion parallelum (simple U), D. helmerseni (expanded base), D. biclavatum (biclavate base), and D. habichi (divergent apertures) as ichnospecies in the suggested classification (Text-Figs. 7.1 & 7.2). D. yoyo and D. polyupsilon are similar in shape but have other different important accessory features.

These differences in shape of the U possibly manifest either ethological differences or morphological differences of the producer organism. However, the slight difference in the shape of the U in the case of D. cincinnatiensis (Osgood, 1970) (Text-Fig. 2.1D) is not an acceptable ichnotaxonomic criterion for use at the ichnospecific level but is retained here for ichnotaxonomic differentiation at the variety level (Table 7.3; Text-Fig.7.2).

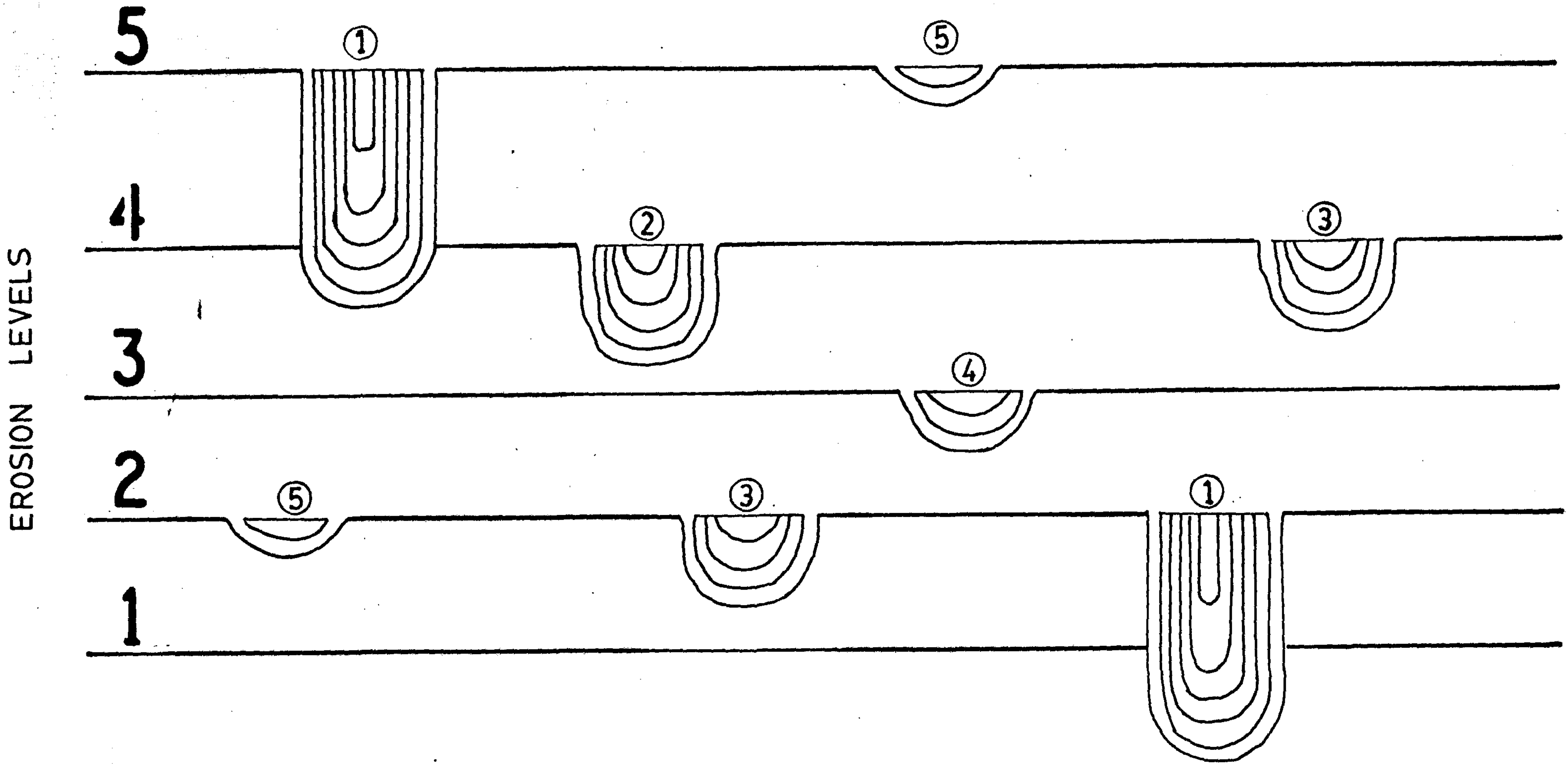
Vertico-lateral shifting of the U-tube within the U-plane: The purely vertical shift of the U-tube results in conspicuously different patterns of spreite, as already discussed. Vertico-lateral shifting of the U-tube within the U-plane is so far only known in association with retrusive spreite and possibly results from fairly high rates of sedimentation or the influence of a prevailing bottom current which forced the animal to adjust the burrow rapidly in conformity with a new or shifting depositional interface. The necessity to shift the burrow might also have been caused by the animal encountering obstacles in its path (e.g., a shell, the presence of different sedimentary structure or even other burrows) Hence, this kind of displacement of the burrow is not believed to manifest genetically important ethological behavior. For this reason this variable is used here for ichnotaxonomic differentiation only at the variety level (Table 2.3).

Morphology of apertures and openings: Various sizes, types, and degrees of inclination of apertures/openings occur in the U-shaped burrows, namely: small, large, vertical-straight, inclined-straight (in the U-plane), and funnel-shaped. Such differences in aperture/opening can manifest environmental influences or preservational aspect (cf. commentary in Table 7.3). For these reasons, aperture/opening type is not regarded here as being useful for ichnotaxonomic differentiation other than at variety level (Table 7.3).

Wall Structure: The structure of the wall/lining in U-shaped dwelling-burrows is designed to prevent burrow collapse, and is therefore functionally appropriate or necessary in all but relatively firm substrates. Multi-layered wall structure occurs in some specimens of Diplocraterion (Goldring, 1962). A burrow lining occurs in all types of subaqueous domichnia and is considered to be a non-specific feature. The need for a lining to the burrow is dependent on the degree of consolidation of the sediment substrate (which is in turn related in part to the sediment grain-size), and the rate of sedimentation. So far no scratch marks have been found (such as occur in Rhizocorallium and Turimettichnus) on the outer wall margin of the vertical U-shaped burrows.

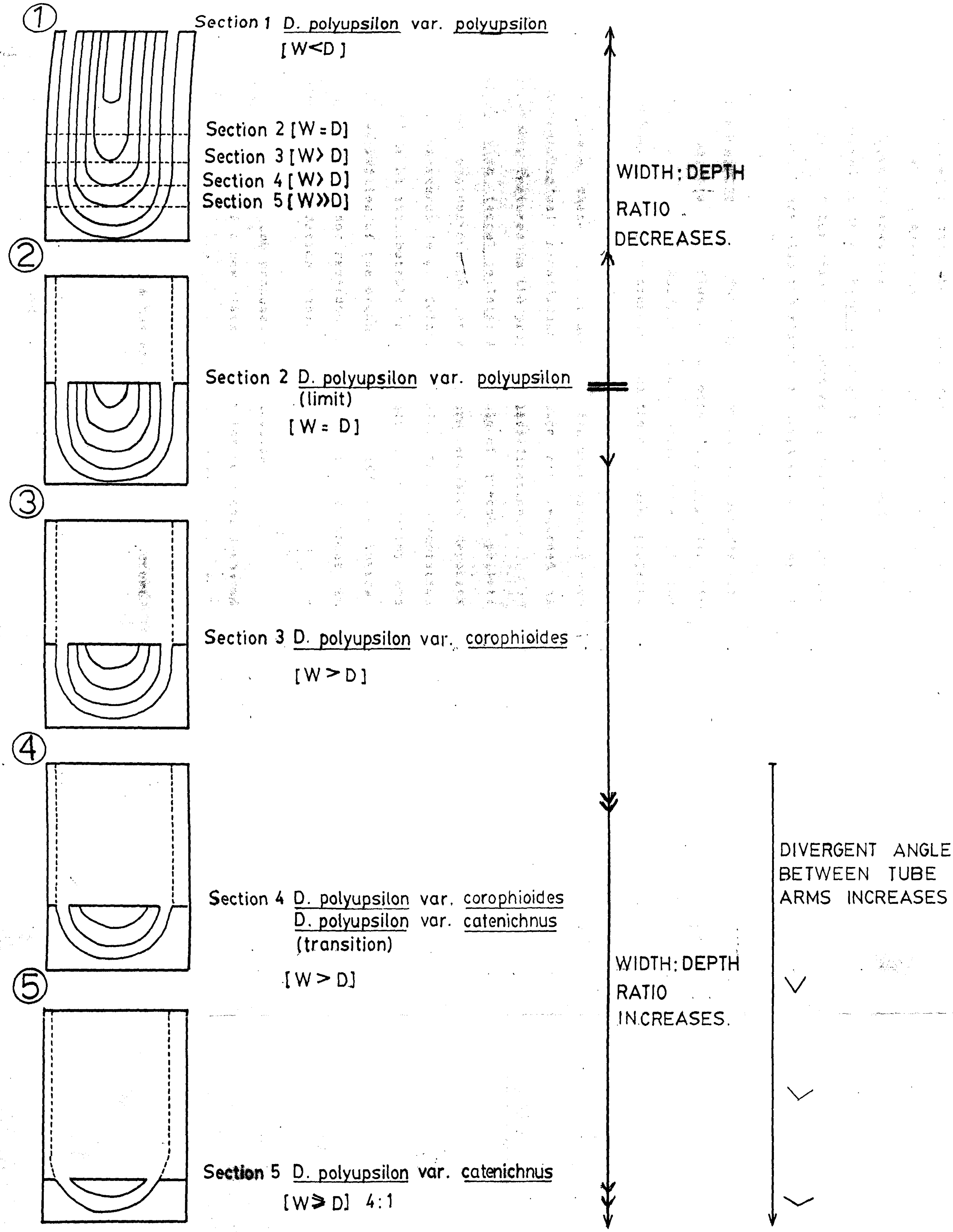
Burrow dimensions and dimensional parameters: The definition of burrow dimensions is given in Table 7.3 and Text-Fig.2.1B. Of these dimensions the width is the only one that has ichnotaxonomic importance. For example, a comparatively larger width characterizes D. polyupsilon and a narrower width characterizes the others (cf. Text-Figs. 7.1D & 7.2). Use of the absolute depth of the burrow is not advisable because it can be an artifact of erosion before or after the animal had vacated the burrow (Text-Fig.2.4). Hence, only in situations where it can be reliably confirmed that the full depth of the burrows has been preserved (or nearly so) can the depth dimension and also the width/depth ratio be confidently used. Even then, the absolute depth dimension is of ichnotaxonomic use only at the ichnospecies and variety levels (Table 7.3). The proposed intra-ichnospecific varietal assignments based on the width/depth ratio in D. Polyupsilon are shown in Text-Fig. 7.5. D. (polyupsilon) catenichnus has a very shallow depth and hence very large width/depth ratio and larger divergent apertural angle near the base of the U-shaped burrow (Text-Fig.7.5). The tube diameter or (in spreite-free forms) the thickness of the burrow increases with depth as the animal grows larger. The "length" dimension of the U-tube as defined by Knox (1973) refers to the curvilinear length measured from the top to the bottom of the tube in situations where the U-plane itself is highly curved, varying from vertical at the top to horizontal at

TEXT-FIG. 7.4. Diagram showing the inferred influence of substrate erosion on the morphology of vertical spreite-bearing U-shaped burrows. Application of the burrow width:depth ratio must be made very carefully, because the dimensions of each of these parameters can be affected by or result from erosion, and hence is potentially prejudicial to the ichnotaxonomic classification. Only in cases where the burrow can be confidently regarded as a fully- or near-intact structure, unmodified by substrate erosion, can it be classified down to variety level. In the proposed classification (Text-Fig. 7.2) the burrow width and depth are regarded as major accessory dimensional parameters of ichnotaxonomic value only at the ichnospecific and variety levels (cf. Table 7.3). In the case of burrows characterized by a very large width/depth ratio, suggesting that such burrows are very likely to represent erosional remnants of formerly deeper burrows, it is recommended that their classification be restricted to the ichnospecific level to avoid synonymy. Burrow morphologies coded 1 to 5 correspond to the five morphological variations of burrow depth shown in Text-Fig. 7.5.



TEXT-FIG. 7.4

TEXT-FIG. 7.5. U-plane sections of five burrows of varying depth (H), uniform width (W), and hence different W/H ratio, arranged in numerically increasing order of W/H downwards. Each of the lower four burrow geometries (i.e., 2 - 5) corresponds to progressively truncated versions of the burrow shown at the top (i.e., burrow 1) as indicated by the numbered transverse sections in the latter. The burrow geometries (1 - 5) correspond to previously named ichnogenera as follows: burrows 1 - 4: *Polyupsilon* (Smith, 1893), (W<D, W=D) and *Corophioides* (Smith, 1893), (W>D); and burrow 5: *Catenichnus* (McCarthy, 1979), (W>>D). W/H relationships as shown in the brackets. Assuming that burrows 2 - 5 are fully- or near-intact forms rather than erosional remnants of formerly deeper burrows, they are renamed here in the proposed classification (Text-Fig. 7.2) as varieties of *Diplocraterion polyupsilon*, as indicated.


①
Section 1 D. polyupsilon var. polyupsilon
[W<D]
Section 2 [W=D]
Section 3 [W> D]
Section 4 [W> D]
Section 5 [W>>D]
WIDTH: DEPTH
RATIO
DECREASES.
②
Section 2 D. polyupsilon var. polyupsilon
(limit)
[W = D]
③
Section 3 D. polyupsilon var. corophioides
[W > D]
④
Section 4 D. polyupsilon var. corophioides
D. polyupsilon var. catenichnus
(transition)
[W > D]
DIVERGENT ANGLE
BETWEEN TUBE
ARMS INCREASES
WIDTH: DEPTH
RATIO
INCREASES.
⑤
Section 5 D. polyupsilon var. catenichnus
[W≥D] 4:1

TEXT-FIG. 7.5

the bottom, in which case the "length' will exceed the "depth". As defined by knox (1973) the "length" therefore is applicable only to U-shaped burrows that are highly inclined and/or whose U-plane is curved (such as Rhizocorallium) and is not applicable to Diplocraterion. Other dimensions such as aperture diameter and U-tube thickness are also important for comparative study of burrow size.

Free tube and plugged tube: These special accessory features (cf. Text-Fig. 7.1D; Plate 36, Figs. a & b) occur in D. yoyo (in the Baggy Beds of England cf. Goldring, 1962), where one arm of the U-tube has been erosionally truncated and the other arm projects upwards into the overlying sediment to the contemporary depositional interface. These kinds of accessory features normally have only sedimentological significance and hence are regarded as minor accessory features in the proposed classification.

Association with faecal pellets: An aureole of faecal pellets occurs around some burrows and can even form laminated deposits around the apertures (e.g., Goldring, 1962). This association would appear to be attributable in most cases to the feeding and excreting activities of the organism that produced the burrow. This association is not regarded as of ichnotaxonomic value in the proposed classification (Table 7.3).

7.2.4. Discussion of the proposed classification

Provision of a new classification for vertical U-shaped burrows is necessary and important because difficulties frequently arise when it comes to the point of assigning ichnogenera and ichnospecies. This problem has arisen because of the accumulation of descriptions of a large number of ill-defined U-shaped burrows in the literature commencing more than a century ago.

Attempts to classify U-shaped burrows in the light of present knowledge about them have been recently made by Osgood (1970), Knox (1973) and Fürsich (1974a). These attempts at classification involved revisions to their taxonomy and had to a decrease in the number of ichnogenera and ichnospecies, many of which were synonymous or poorly defined and differentiated.

The classification proposed here (Text-Fig. 7.2) attempts to eliminate the remaining problems by clarifying the significance of important morphological features of the U-shaped burrows the higher ichnotaxonomic levels as well as the less important accessory features at the lower ichnotaxonomic levels. Some of the features illustrated in Text-Fig. 7.2. cannot be regarded or used as taxonomic characteristics because they really are not genetically related to the burrows produced by the organism but are simply artifacts either of penecontemporaneous preservational aspect, sedimentation, or modern weathering and erosion.

The proposed classification (Text.Fig. 7.2) is applicable only to spreite-bearing vertical burrows. In this classification all vertical spreite-bearing U-shaped burrows are assigned to the ichnofamily Diplocrateriidae. This classification excludes from this ichnofamily all horizontal-to-shallowly-inclined U-shaped spreite-bearing burrows which are here assigned to the ichnofamily Rhizcoralliidae as well as the vertical spreite-free _Arenicolites_ Salter, 1857. _D. parallelum_ (Torell, 1870), selected by Richter (1926, p.213), is the type species of the Diplocrateriidae. Within this group there are two major subgroups distinguished by the width of the burrow and also by the nature of the pattern of spreite as seen in the U-plane.

Burrows belonging to the first group (i.e. the D. Parallelum group in Text-Fig.7.2) are characterized by a narrow burrow width and number five significant species separated on the basis of the outline of the burrow in the U-plane section (Text-Fig. 7.2). The type species of this group, D. parallelum (Torell, 1870), has parallel arms with narrow funnel apertures and is here termed D. parallelum var. parallelum. A second variety, D.parallelum var. lyelli (Torell, 1870), can be differentiated by its wider funnel-shaped apertures. The second species, D. helmerseni (Opik, 1929), is characterized by an expanded base and has the additional variety D. (helmerseni) var. cincinnatiensis (Osgood, 1970) characterized by a U-shaped burrow with outwards-inclined arms in addition to an expanded base. The third species, D. biclavatum (Miller, 1875), is uniquely different to the others since it has a biclavate base (i.e., two arms extending downwards from the base of the U-tube; Text-Fig.7.2). This latter type of morphology may indicate a different kind of producer organism of this burrow relative to the other types. The fourth species, D. habichi (Lisson, 1904), is defined by divergent arms in the upper (apertural) part of the tube. D. yoyo (Goldring, 1962) is defined by having bidirectional spreite and an accessory plugged tube (cf. Text-Fig. 7.1).

The second major group, i.e., the D. polyupsilon (Smith, 1893) group (Text-Fig.7.2) is characterized by a larger width than species in the D. parallelum group and a uniquely distinctive U-in-U pattern of spreite. The type species and variety, D. polyupsilon var. polyupsilon (Smith, 1893) has as a smaller width/depth ratio than all the other varieties of D. polyupsilon (cf. Text-Figs. 7.2 & 7.5), namely: D. polyupsilon var. corophioides (Smith, 1983), D. polyupsilon var. luniformis (Blanckenhorn, 1917), and D. polyupsilon var. catenichnus (McCarthy, 1979). The variety D. polyupsilon var. rosei (Dahmer, 1937) is unique within the D. polyupsilon group in having exclusively protrusive spreite (Text-Fig. 7.2) which may reflect animal response to erosion of the substrate. The width/depth ratio of the burrow is taxonomically very important in the D. polyupsilon group where it can be demonstrated or confidently inferred that the preserved depth of the burrows has not been reduced by erosion (cf. Text-Figs. 7.4 & 7.5). It would seem that, on the basis of a small number of examples of D. polyupsilon in the present study area and on the basis of observations of others in the literature of this trace fossil, that the degree of erosional reduction of the burrows' depth is difficult to determine. In cases where the degree of erosional reduction of the burrow depth is believed to be large it is suggested that the burrow be assigned only to the specific level of the classification. The morphological length of the producer animal on the other hand can be expected to affect the depth of the burrow (Fürsich, 1974), but it is difficult to resolve even what kind of animal produced the burrows of the D. polyupsilon group, and not all deep U-shaped burrows were necessarily produced by elongated

TABLE 7.4. Original and revised ichnotaxonomic name of vertical spreite-bearing U-shaped burrows in terms of the proposed new classification (cf. Text-Fig. 7.2).

Original (previous) name	**New (proposed) name**
(1) Diplocraterion parallelum (Torell, 1870).	D. parallelum var. parallelum (Torell, 1870).
D. lyelli (Torell, 1870).	D. parallelum var. lyelli (Torell, 1870).
(2) Corophioides helmerseni (Opik, 1929).	D. helmerseni var. helmerseni (Opik, 1929).
C. cincinnatiensis (Osgood, 1970).	D. helmerseni var. cincinnatiensis (Osgood, 1970).
(3) Arathraria biclavata (Miller, 1875).	D. biclavatum (Miller, 1875).
(4) Tigillites habichi (Lisson, 1904).	D. habichi var. habichi (Lisson, 1904).
Polyupsilon coloradoensis (Howell, 1957).	D. habichi var coloradoensis (Howell, 1957).
(5) D. yoyo (Goldring, 1962).	D. yoyo (Goldring, 1962).
(6) Corophioides polyupsilon (Smith, 1893).	D. polyupsilon var. polyupsilon (Smith, 1893).
C. polyupsilon (Smith, 1893).	D. polyupsilon var. corophioides (Smith, 1893).
C. rosei (Dahmer, 1937).	D. polyupsilon var. rosei (Dahmer, 1937).
(7) Arenicoloides luniformis (Blanckenhorn, 1917).	D. polyupsilon var. luniformis (Blanckenhorn, 1917).
Catenichnus contentus (McCarthy, 1979).	D. polyupsilon var. Catenichnus (McCarthy, 1979).

animal.

The ichnotaxonomic reassignments (at generic, specific and variety levels) of vertical spreite-bearing U-shaped burrows are summarized in Table 7.4 using the original name of each of the forms concerned.

7.2.5. Diplocrateriids in the Lower Permian of the southern Sydney Basin

Burrows of Diplocraterion parallelum (Torell 1870) are abundant in tidal and shallow subtidal sandstones of the Pebbley Beach Formation and the Wasp Head Formation of the southern Sydney Basin (McCarthy, 1979). According to McCarthy (1979, p.356-357), most of the specimens exhibit incipient protrusive spreite and only a very few possess conspicuous protrusive spreite. The size and shape of these burrows resemble those of D. yoyo (Goldring, 1962) and exhibit much smaller tube diameters than are characteristic of D. parallelum and D. lyelli (Torell, 1870).

Vertical spreite-bearing shallow catenary-shaped burrows referred to a new ichnotaxa, Catenichnus contentus McCarthy (1979), also occur in these same formations. These are characterized by a very wide limb or zone of spreite and by walls lined by dark clayey material; retrusive spreite are characteristic but protrusive spreite are also present in some specimens. The catenary-shaped tube of these burrows has an oval or circular outline in transverse cross-section, and the tube openings/?apertures are described by McCarthy (1979, p.357) as divergent and expanded. The depth/width ratio is less than 1:4

and the width of the tube between apertures is 15-25 cm (McCarthy 1979, p.357-358).

Catenichnus is strongly divergent at the opening of the tube and this is a significant feature also present in D. habichi (= Tigillites habichi Lisson, 1904). In my opinion, the divergent nature of the openings/?apertures shown in McCarthy's illustrations (i.e., his text-figs. 9a, 10a-d; & plate 1, figs. 4-6) is apparent rather than real and seems to be an artifact of erosion which has cut through to the base of what were formerly U-shaped burrows (cf. Text-Figs. 7.4 & 7.5) removing the top part of the burrows and leaving behind the basal parts to define very broad and shallow catenary traces. The divergent angle between the arms of the catenary increase towards the base of the burrows and, viewed as shallow erosional remnants of formerly deeper burrows, the width/depth ratio will also increase with increasing loss of the upper part of the burrow through erosion (cf. Text-Fig. 7.4). Most of the other features described by McCarthy (1979) in respect of his new ichnotaxon Catenichnus contentus are also present in D. polyupsilon (Smith, 1893), a symmetrical U-shaped burrow, and in D. polyupsilon var. luniformis (Blanckenhorn 1917) which possesses divergent apertures as originally described by Blanckenhorn (1917). Therefore, in my opinion, Catenichnus contentus McCarthy (1979) should be regarded as a junior synonym of Diplocraterion (Torell, 1870); in particular it includes all significant features of D. polyupsilon var. corophioides (Smith 1893). In the proposed classification (Text-Fig. 7.2) it is differentiated from D. polyupsilon var. corophioides (Smith, 1893) on the basis of its large divergent angle and large width/depth ratio (which is greater than 4:1) and becomes *D. polyupsilon* var. *catenichnus* (McCarthy, 1979) (cf. Table 7.4; Text-Figs. 7.2 & 7.5). This revision of the ichnotaxonomic status of *Catenichnus contentus* McCarthy (1979) in the proposed classification is made on the assumption that this burrow is indeed an essentially fully developed and fully preserved shallow burrow and not simply an erosional remnant of a formerly deeper U-shaped burrow. Consequently, only on the basis of this assumption can the proposed variety names given in Text-Figs. 7.2 and 7.5 be regarded as legitimate. The rationale behind this approach is that it is better not to assign an ichnogeneric name to intact U-shaped burrows characterized by shallow depth whose other morphological characteristics are essential identical to those of a securely established ichnogenus. Rather, it is preferable to regard them as varieties of that ichnogenus and to name them accordingly (cf. Text-Figs. 7.2 & 7.5; Table 7.4). However, if such shallow are indeed erosional artifacts of formerly deeper burrows (cf. Text-Fig. 7.4), then it is preferable that they be ichnotaxonomically assigned only at the species rather than variety level.

Diplocraterion has also been recorded from the Snapper Point Formation (Lower Permian) in the southern Sydney Basin by Carey (1978). However, she did not describe it very fully, referring to her specimens simply as vertical spreite-bearing U-shaped burrows. She described the spreite in these burrows as disturbed and re-ordered sediment layers and the arms of the U-tubes as being confluent.

7.2.6 Diplocrateriids of the Sydney Northshore Triassic

Three representative ichnospecies of Diplocraterion are recorded here from the study area: D. parallelum and D. yoyo occur at Little Head and D. polyupsilon (two varieties) occurs at Bungan Head and at Bilgola Head.

7.2.7. Systematic ichnology of the Diplocrateriidae

Diplocraterion Torell, 1870.

Diplocraterion parallelum Torell, 1870, p.13.
Diplocraterion lyelli Torell, 1870, p.13.
Corophioides polyupsilon Smith, 1893, p.282, pl.10.
Tigillites habichi Lisson, 1904, p.31-43. figs.11-18, & 21.
Polyupsilon coloradoensis Howell, 1957, p.151-152, pl.16, figs.2 & 3.
Arenicoloides luniformis Blanckenhorn, 1916, p.36-40.
Diplocraterion yoyo Goldring, 1962, p.235-245
Arthraria biclavata Miller, 1875, p.354, fig.26.
Corophioides helmerseni Opik, 1929, p.33-34, fig.4, pl.1 (figs.3 & 4).
Corophioides cincinatiensis Osgood, 1970, p.321-323, figs.8 & 29, pl.60 (figs.1, 5 & 8), pl.61 (figs.4, 6 & 8), pl.62 (figs.3, 4 & 6), and pl.63 (fig.4).

Type species: D. parallelum

Torell, 1870, p.13 (designated by Richter, 1926, p.213).

Diagnosis: Vertical spreite-bearing U-shaped dwelling-burrows of suspension-feeders.

Remarks: U-shaped burrows with unidirectional or bidirectional (protrusive and/or retrusive), regular or irregular, laterally continuous or discontinuous spreite; the arms of the U-tube are variously parallel or are characterized by an outward inclination at the bottom or the top of the U; the aperture/opening is either straight or funnel-shaped, and either small or large.

Comparison: Diplocraterion vs. Corophioides

Some workers, e.g. Knox (1973), have regarded Corophioides as a junior synonym of Diplocraterion on the basis of the presence/absence of funnel-shaped apertures which were believed to be present only in species of Diplocraterion and absent in Corophioides. However, modifications of the apertural part of the burrow can occur post-mortem and hence apertural features should not be used as ichnotaxonomically diagnostic attributes. The shape of the aperture is regarded as only an accessory feature in the proposed classification and cannot be used to separate ichnogenera. Therefore, Corophioides Smith, 1893, must be regarded as a junior synonym of Diplocraterion Torell, 1870, the latter having priority.

Comparison: Diplocraterion vs. Polyupsilon

Goldring (1962) and Frey & Chowns (1972) equated these two forms as belonging to the same genus and regarded them as synonyms, but Hantzchel (1962) separated them into two different ichnogenera. The difference between the two forms is not only in the size of the burrows but also in respect of accessory features: in particular, one species of Diplocraterion (i.e., D. habichi Lisson, 1904) has divergent arms at the top of the U. Because this difference is regarded as of subsidiary importance in the proposed classification, separation of the two forms into different ichnogenera on this basis is not warranted. Moreover, except for the contrast in spreite pattern between these two forms (i.e., U-in-U in Polyupsilon and U-above-U in Diplocraterion: cf. Text-Figs. 7.1 & 7.2) all other morphological features in the two forms are essentially the same. Consequently, there is no reason to retain Polyupsilon Howell (1957) as a separate ichnogenus and it is argued here that it is more logical to regard it as a species of Diplocraterion (cf. Text-Fig. 7.2).

Comparison: Diplocraterion vs. other burrows

The U-shaped burrows of Arenicolites Salter (1857) can be separated from those of Diplocraterion on the basis of their lack of spreite. Rhizocorallium Zenker (1836) is also a U-shaped spreite-bearing burrow but is orientated obliquely or parallel to the bedding plane (Text-Fig. 7.2).

D. parallelum Torell, 1870.

Type species: D. parallelum Torell, 1870, p.13 (designated by Richter, 1926, p.213).

Diplocraterion parallelum var. parallelum (Torell, 1870).

Plates 36, Figs. a - e
37, Figs. a - c
38, Figs. a - c

Diagnosis (specific assignment): U-shaped burrows with parallel arms, disposed almost vertically and in most cases possessing protrusive spreite. The apertures are well defined and funnel-shaped.

Remarks (diagnostic features): U-shaped burrows with parallel arms, distinct but thin wall, and small funnel-shaped apertures with circular outline. The spreite are mostly protrusive and regular, laterally continuous, rarely discontinuous, and with characteristic U-above-U pattern, narrow width and small thickness (cf. detailed dimensional data in Table 7.5A).

Description: Protrusive form (unidirectional spreite). Most of the transverse sections which cut through the spreite show a dumbbell-shaped outline with two circular apertures clearly separated from the narrow limb of spreite (Plate 36 Fig. c &

Plate 37 Figs. a - c). Some other transverse sections which intersect the U-structure above the spreite (i.e., at the level of the free tubes) exhibit the apertures as two unconnected circular or semicircular outlines (Plate 37 Figs. a - c). The spreite generally are developed in the lower part of the burrow and are considerably narrower throughout the midline of the limb as shown in the transverse sections (Plate 37 Fig. c). Deflected and irregularly developed spreite are observed in some transverse sections (Plate 38 Figs. a & c) and this type of spreite development presented difficulties in measurement of the nearest neighbor when measuring from the midpoint of the limb (i.e., measurement F in Text-Fig. 7.6). The spreite laminae are convex-downwards in the U-plane section (Plate 36 Fig. d). In median section (Plate 36 Fig. e), the spreite occur as straight to slightly irregular well-defined zones of generally uniform thickness. The base of the U-tube is semicircular as seen in the U-plane. In some burrows the width at the base of the U is a little smaller than at the top of the burrow (Plate 36 Fig. d). The wall is well defined, being readily distinguished from the host sediment by its relatively darker colour. No special ornamentation is observed on the burrow surface. The apertures of the tubes are well defined and are funnel-shaped in transverse section (Plate 37 Fig. c).

Comparison: Plugged tubes occur in some specimens of D. parallelum from the study area (Plate 36 Figs. a & b) like those which characterize D. yoyo Goldring (1962), but, unlike the latter, most burrows of D. parallelum show unidirectional (protrusive)

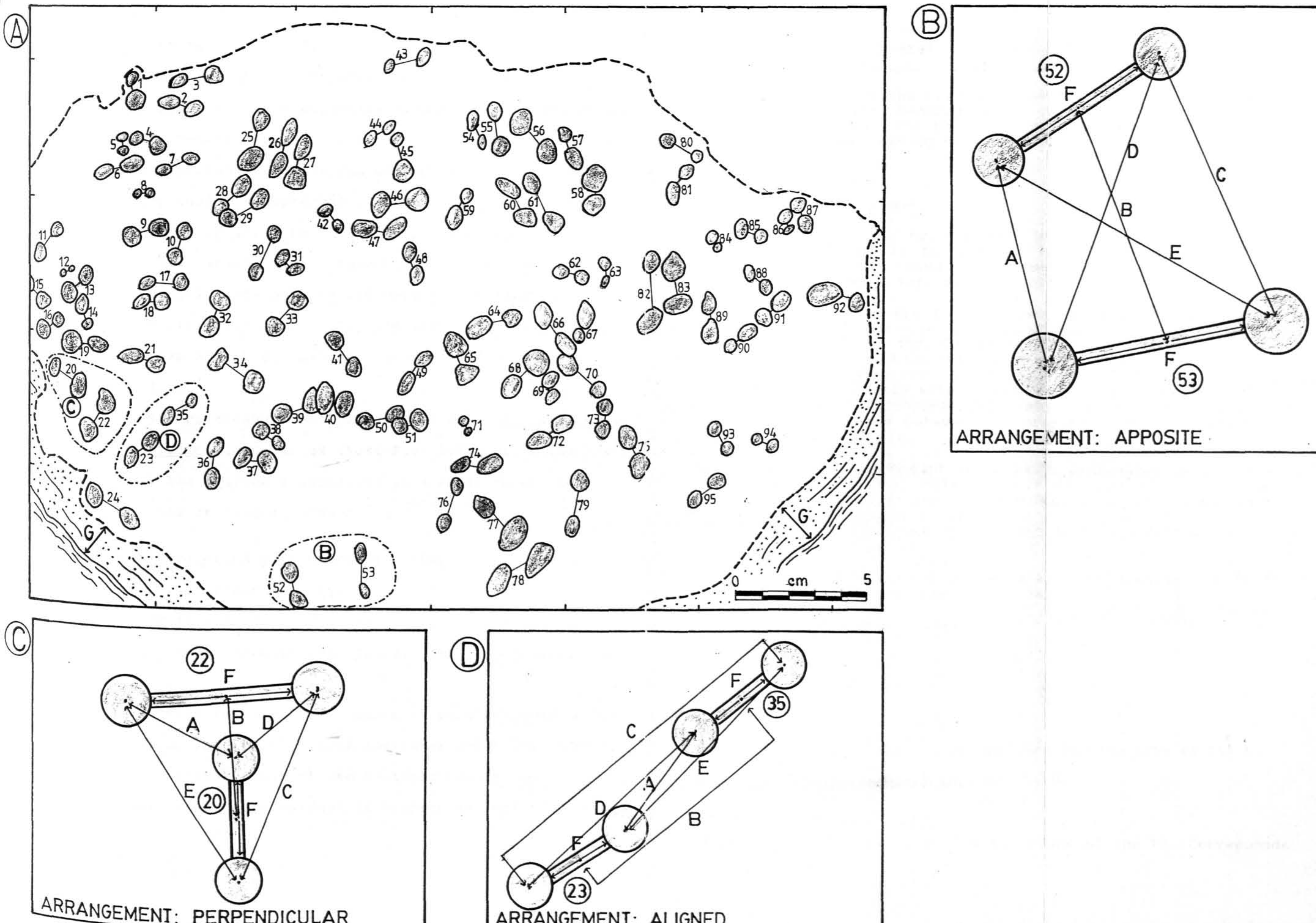
TEXT-FIG. 7.6. Diagrams illustrating application of the distance-to-nearest-neighbour (DNN) method used in bedding-plane exposures of the vertical U-shaped burrows of <u>Diplocraterion</u>.

A. Overlay drawing of a slab of rock (1205/MU.44443) from trace fossil subinterval ID2.1 of the Lower Newport Member, Little Reef area (shown also in Plate 37). The actual rock slab comprises two sandstone beds and an intervening thin bed of siltstone (cf. Table 7.5) and the overlay drawing shown here was made on the top surface of the top sandstone bed (of thickness G in diagram). Each U-shaped burrow is identified in the diagram by a line connecting its paired openings. In most cases these paired openings are connected by a limb of spreite (not shown in diagram but evident in Plate 37). In a minority of other cases of burrows lacking spreite (due to the section exposing the free tubes at the top of the U) the paired identity of various openings is clearly evident on the basis of matching opening diameters and the relative spacing of the openings (cf. Plate 37, Fig. c). No ambiguous identity relationships of burrow openings occur in actual fact in this rock slab. Numbers beside each set of paired openings record the burrow count in the population density exercise (cf. Table 7.6). Pairs of burrows (B, C, & D) enveloped by dashed lines at bottom-left exemplify particular geometrical arrangements corresponding to idealised situations shown in diagrams B, C, and D respectively. The population density of the burrows exposed on this bedding plane using the DNN method employed the distance parameter B as defined in diagrams B, C, and D (rather than any of the other distance parameters defined therein) because these are believed to have been dwelling-burrows rather than feeding-burrows (cf. rationale discussed by Pemberton & Frey (1984) and Schäfer (1972)).

B, C & D. Definition diagrams of different distance parameters that can be used in DNN studies of vertical U-shaped burrows as originally defined by Pemberton & Frey (1984, fig. 4). Each diagram shows the paired openings (linked by the double line) of two U-shaped burrows in apposite, perpendicular and aligned arrangements (cf. enveloped burrows B, C and D respectively in diagram A. `F' is the distance between the proximate margins of the U-tube (= length of limb where spreite is present/exposed). Distance parameters A to E (cf. Pemberton & Frey, 1984, fig. 4). are defined in the same way in each diagram as follows.

A: distance between two close-adjacent apertures/openings.
C: distance between two far-adjacent apertures/openings.
B: distance between midpoints of burrow limbs.
D & E: distance between two diagonal opposed apertures/openings.

As emphasised by Pemberton & Frey (1984) parameter B is the most appropriate distance measurement applicable in the case of the domiciles of suspension-feeding infauna, and the parameters A and C - E are appropriate in the case of the domiciles of deposit-feeding infauna because of the different uses to which one of the tubes (or more exactly, one end of the tube) is put in the case of the latter, namely for faecal storage rather than feeding.


A
B
C
D
0 cm 5
ARRANGEMENT: APPOSITE
ARRANGEMENT: PERPENDICULAR
ARRANGEMENT: ALIGNED

TEXT-FIG. 7.6

spreite rather than bidirectional spreite. As in D. yoyo, the apertures/openings are all funnel-shaped. Associated faecal pellets have not been observed.

Studied material: Specimens 1214/MU.44451 and 1216/MU.44453.

Distribution: Specimens were collected from the lower part of the Lower Newport Member at Little Head (area 7), especially from beds of fine sandstone commonly exhibiting parallel-stratification in trace fossil subinterval ID2. D. parallelum does not occur elsewhere or in any other trace fossil subinterval.

Preservation and association: These burrows are preserved as full-relief forms in beds of fine and very fine sandstone characterized by parallel-lamination. They are associated with D. yoyo and other burrows of the J-, L-shaped and flask-shaped categories (see Chapter 17).

Ichnofacies and palaeoenvironmental affinities: D. parallelum belongs to Skolithos ichnofacies (Text-Fig. 3.5) and in the study area occurs within sediments deposited in a sandy shoreline in a shallow estuarine or coastal lagoon.

Diplocraterion yoyo Goldring, 1962.

Plate 37, Figs. a - c

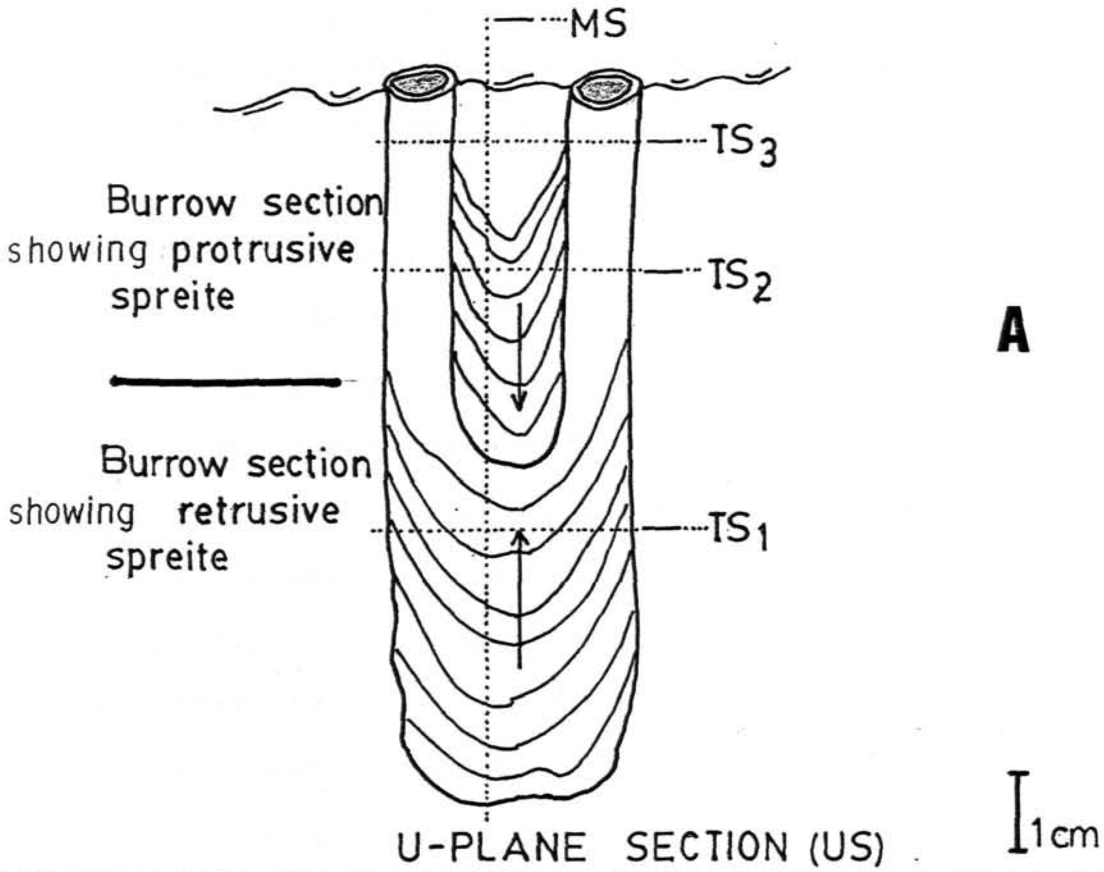
Diagnosis (specific assignment): U-shaped burrow with parallel arms, bidirectional spreite and funnel-shaped apertures with plugged tubes.

Remarks (diagnostic features): U-tubes with parallel arms, a thin indistinct wall, and funnel-shaped apertures which are circular in transverse section. Most of the U-shaped burrow exhibit one plugged tube, especially evident in outcrop as small elevated

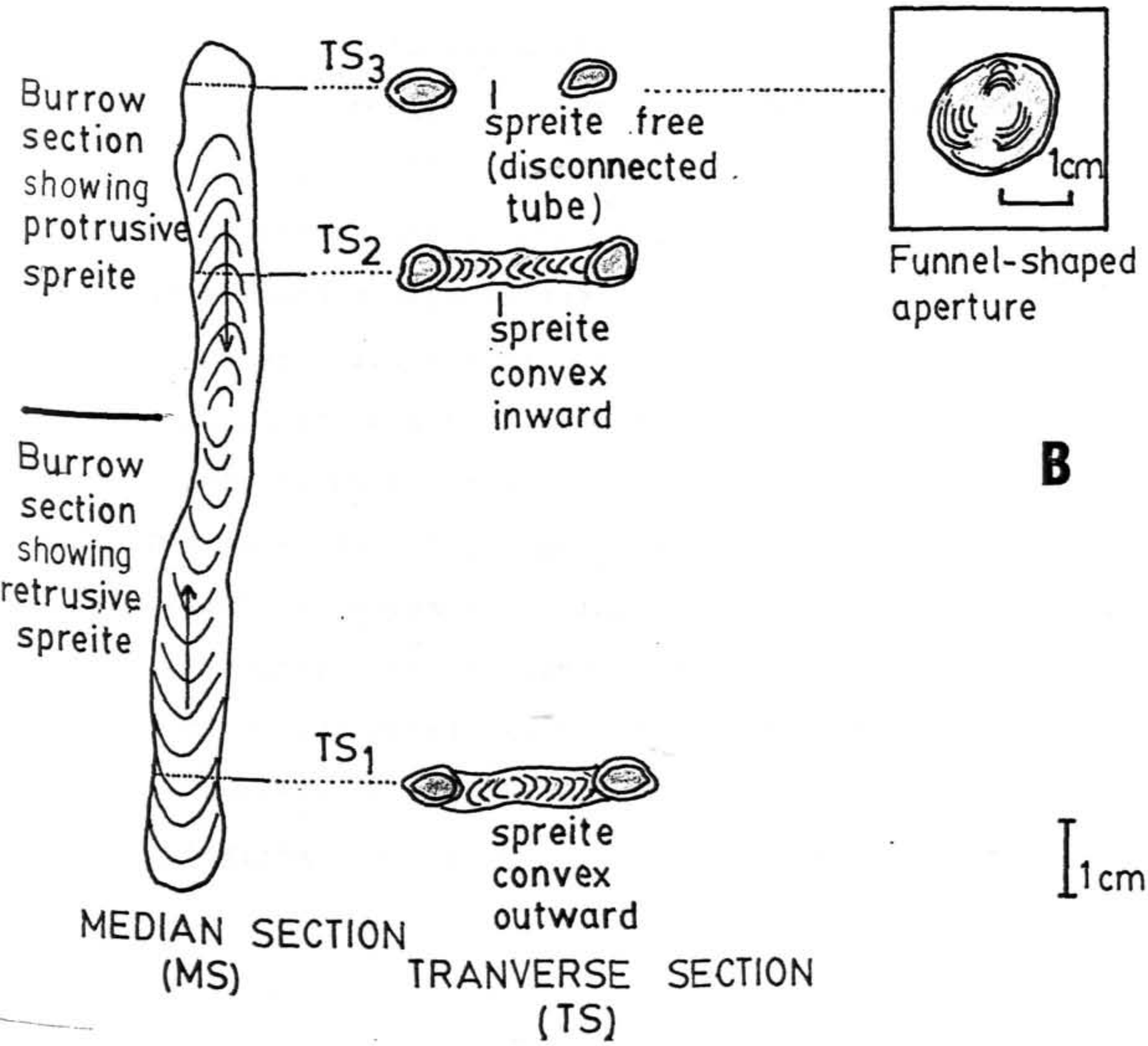
TEXT-FIG. 7.7. Different cross-sections of _Diplocraterion yoyo_ Goldring (1962) showing protrusive (PS)/retrusive (RS) spreite relationships based on sample 1205/MU.44443 (cf. Plate 37).

A. Three-dimensional diagram showing U-plane and transverse sections. Protrusive spreite preserved in top half of burrow and retrusive spreite and base of U-tube preserved in lower half of burrow. Drawing is based on a natural exposure of an individual burrow (Plate 36, Figs. f & g).

B. Median section (MS) and three transverse sections (TS1 to TS3) cut at progressively higher levels upwards from the base of the burrow, as indicated. In the median section the convex-upward spreite is protrusive and concave-upward spreite is retrusive. Similarly, in transverse section, the protrusive spreite is convex inwards (TS2) and the retrusive spreite is concave inwards (TS1) (cf. Text-Fig. 7.1C). Transverse section TS1 is cut through the free tubes and hence is spreite-free. Median section is based on a natural exposure of an individual burrow but transverse sections TS1 and TS3 are based on natural sections through different burrows at different levels. Drawing of the apertural funnel in box is enlarged from TS3.



MS
TS3
TS2
TS1
Burrow section showing protrusive spreite
Burrow section showing retrusive spreite
A
U-PLANE SECTION (US)
1cm



TS3
TS2
TS1
Burrow section showing protrusive spreite
Burrow section showing retrusive spreite
spreite free (disconnected tube)
spreite convex inward
spreite convex outward
1cm
Funnel-shaped aperture
B
1cm
MEDIAN SECTION (MS)
TRANVERSE SECTION (TS)

TEXT-FIG. 7.7

mounds. The spreite pattern is quite uniquely bidirectional, mainly retrusive in the lower part and protrusive in the upper part.

Description: The burrows exhibit both protrusive and retrusive (i.e., bidirectional) spreite. The U-plane section in Plate 36 Figs. f and g, shows that the spreite are partly deflected, especially in the upper protrusive section. As seen in the U-plane section the arms of the U are almost straight to slightly curved cylindrical tubes joined together to form a semicircular base (cf. Text-Fig. 7.7). The individual spreiten laminae are ill-defined (especially in the retrusive part) but they are still sufficiently clear to be discernibly convex-downward and to reach to the distant wall margin (Text-Fig. 7.7). The upper protrusive part of the burrow exhibits more clearly defined spreite which are also convex-downwards but only reach to the proximate wall margin. The apertures are well defined and are funnel-shaped but not of equal diameter. No free-tubes have been observed but, one opening of one burrow is plugged (Plate 36 Fig. a). Wall margins (both proximate and distant) are not well defined but are nevertheless discernible because of the colour contrast between the purplish sandstone infills of the tubes and the white sandstone of the host rocks.

Comparison: The most significant feature of this species is the bidirectional movement of the organism during its dwelling stage. The formation of the spreite is uniquely bidirectional, partly retrusive and partly protrusive. According to Goldring (1962), this pattern of spreite development reflects changes in the environmental parameters. During the dwelling phase, the environment may change in terms of rate of degradation (erosional stripping of sediment) or sedimentation. Consequently, the organism will attempt to maintain its optimum depth by moving upwards upon deposition or downwards in response to erosion. Some problematic U-tubes in the study area that are either incompletely preserved or incompletely exposed exhibit exclusively unidirectional spreite. Hence, whether or not the spreite in the lost on hidden part of the burrows had/have the same polarity as that in the preserved/exposed part is difficult/impossible to resolve. In such cases it is therefore suggested that ichnotaxonomic assignment of the burrow be restricted to the generic level. This problem occurs especially where burrows of these two ichnospecies (i.e. D. parallelum and D. yoyo) occur together, as in the present case.

Studied material: Specimens 1210/MU.44448 and 1205/MU.44443.

Distribution: The Samples were collected from Little Reef (area 12) where they occur in trace fossil subinterval ID2 in the Lower Newport Member. As far as is known D. yoyo does not occur in any other trace fossil subinterval, nor at any other localities.

Preservation and association: D. yoyo occurs as full-relief dwelling-burrows associated with D. parallelum var. parallelum, unclassified burrow networks, and flask-, J-, and L-shaped burrows.

Ichnofacies and palaeoenvironmental affinities: D. yoyo belongs to the Skolithos ichnofacies (Text-Fig. 3.5) and in the study area colonized the sandy shoreline of a shallow, fluvially-dominated brackish-marine coastal lagoon or estuary.

TABLE 7.5A. Representative measurements (cm) of <u>Diplocraterion parallelum</u> and <u>D. yoyo</u>. See Table 7.5B for explanation of abbreviations.

Sample no. 1205/MU.44443 <u>D. parallelum</u>

No.	W	H	W/H	T	Dm d1	Dm d2	Dm d	Code no. on sample		Type of section
1	2.30	x	x	0.50	0.78	0.66	0.72	49		TS
2	2.38	x	x	0.72	1.02	0.82	0.92	11		TS
3	2.47	x	x	0.62	1.15	1.55	1.35	77	cf.	TS
4	2.38	x	x	0.68	0.82	0.66	0.74	36	Text-	TS
5	2.47	x	x	0.76	0.91	0.99	0.95	15	Fig.	TS
6	2.57	x	x	0.94	0.78	1.00	0.89	65	2.6A	TS
7	2.46	x	x	0.96	0.91	0.92	0.92	33		TS
8	2.45	x	x	0.85	1.45	1.04	1.25	19		TS
9	2.48	x	x	0.73	0.91	0.94	0.93	45		TS

Sample no. 1210/MU.44448 <u>D. parallelum</u>

No.	W	H	W/H	T	Dm d1	Dm d2	Dm d	Code no. on sample	Type of section
10	2.72	x	x	0.60	0.67	0.68	0.68	-	TS
11	2.25	x	x	0.61	0.78	0.89	0.84	-	TS
12	2.44	8.91	0.27	0.70	0.88	0.94	0.91	-	US
13	2.3	9.25	0.25	0.62	0.92	0.71	0.80	-	US
14	2.28	x	x	0.68	0.64	0.68	0.66	-	TS
15	2.78	x	x	0.90	1.08	0.91	1.00	-	TS
16	2.07	8.72	0.24	0.77	0.68	0.88	0.78	-	US
17	3.00	x	x	0.64	0.99	0.80	0.90	-	TS
18	2.33	x	x	0.69	0.85	0.60	0.73	-	TS
19	2.55	8.06	0.32	0.75	1.10	0.90	1.00	-	US

Sample no. 1214/MU.44451 <u>D. parallelum</u>

No.	W	H	W/H	T	Dm d1	Dm d2	Dm d	Code no. on sample	Type of section
20.	1.98	(top)							
	1.53	(bottom)							
Avg.	1.76	13.5	0.13	1.02	1.28	1.50	1.39	-	US
21	x	14.5	x	0.90	x	x	0.90	-	MS
22	x	13.5	x	1.15	x	x	1.15	-	MS

Sample no. 1205/MU.44443 <u>D. yoyo</u>

No.	W	H	W/H	T	Dm d1	Dm d2	Dm d	Code no. on sample	Type of section
1	2.75	11.6	0.24	0.71	0.95	0.66	0.81	96	US
		11.6	(Dsr)					(on edge)	
		9.2	(Dsp)						

	W	T	d	H
n	= 20	= 22	= 22	= 7
σ(n)	= 0.21	= 0.156	= 0.197	= 2.56
σ(n-1)	= 0.257	= 0.159	= 0.202	= 2.77
$\bar{x}$	= 2.42	= 0.763	= 0.928	= 10.92
Σx	= 48.44	= 16.79	= 20.41	= 76.44
Σx2	= 118.58	= 13.35	= 19.79	= 880.70

TABLE 7.5B. Representative measurements (cm) of Diplocraterion polyupsilon.

Sample no. 1005a/MU.44426 D. polyupsilon var. corophioides

No.	W	H	W/H	T	Dm d1	Dm d2	Dm d	Code no. on sample	Type of section
1	7.30	<5	1, 1<	0.62	1.07	0.95	1.01	-	TS
2	5.32	"	"	0.87	0.63	0.70	0.67	-	TS
3	4.72	"	"	0.75	1.00	0.86	0.93	-	TS
4	6.57	"	"	0.73	0.84	0.58	0.71	-	TS
5	4.48	"	"	0.80	0.58	0.71	0.65	-	TS
6	5.55	"	"	1.14	1.02	0.83	0.93	-	TS
7	5.45	"	"	1.03	1.07	1.33	1.20	-	TS

	W	T	d
n	= 7	= 7	= 7
σn	= 0.85	= 0.17	= 0.19
σ(n-1)	= 0.92	= 0.18	= 0.20
$\bar{x}$	= 5.59	= 0.85	= 0.87
Σx	= 39.09	= 5.94	= 6.10
Σx2	= 223.32	= 5.24	= 5.57

Abbreviations

W = Width or Length.
T = Thickness or breadth.
Dm = Diameter of a tube.
d1 = Diameter of aperture one.
d2 = Diameter of aperture two.
d = Average.
H = Depth of the U tube.
Dsr = Depth of spreite in retrusive part.
Dsp = Depth of spreite in protrusive part.
TS = Tranverse section.
US = U-plane section.
MS = Median section.

1. All the specimens studied here are characterised by retrusive spreite and because of their extensive retrusion, the shape and diameter of the apertural openings are commonly disfigured as shown by the variation of values of d1 and d2.

2. The thickness of the bed containing the trace fossils is about 5 cm (Plate 39 Figs. b & c). The actual measurements were made on a loose slab of the bed in which no traces of the burrows are evident on the under-side. Hence, the actual depth (H) of the burrows must be less than the thickness of the bed which is 5 cm. The calculation of the W/H ratio will be within the range of 1 or more than 1, which is within the range of D. polyupsilon var. corophioides (1 or W>D) (cf. Text Fig. 7.5).