PART 2

SYSTEMATIC ICHNOTAXONOMY

IMPORTANT NOTES RELATING TO THE SYSTEMATIC ICHNOTAXONOMY IN PART 2

Ichnotaxonomic description of each trace fossil described in Part 2 of this volume is organized in the following order of subheadings in order to avoid repetition and to maintain clarity of important ichnological values of the ichnotaxon.

Diagnosis (taxonomic assignment): Generic/specific/varietal/type assignment concerned only with the defined (probably well-defined) particular characteristics that can be assigned to the ichnotaxon, with or without emendation.

Remarks (diagnostic features): Concerned with all morphological characteristics of the burrows or traces (which are relatively well-defined) and not restricted only to the morphologic characteristics of taxonomic value. This description of the characteristics does not include interpretation of the animal's behavior or ethology.

Description (and ethology/associations): Concerned with all the morphological characteristics (but emphasizing more particularly those of diagnostic character) with their relevant behavioural responses to the conditions of the environments and to the associated other (burrowing) organisms. Both scaler and vector measurements are also included here. Interpretation of these scaler or vector measurements, population-density studies and their relevant palaeoenvironmental significance are also discussed here.

Comparison: Discussion regarding other known related ichnotaxa (both morphology and ethology). The discussion here is both descriptive (ichnotaxonomic) and ethological.

Studied material: The studied material described with field collection number and Macquarie University catalog number if the sample has been retrieved from the field. Some specimens which were not retrieved from the field are described and abbreviated NRFF (not retrieved from the field), especially in plate descriptions.

Distribution: Distribution of the studied ichnotaxon is described here in terms of its stratigraphic extent (i.e., trace fossil interval, subinterval, or level) and geographic extent (studied locations with name and code number of the headland).

Preservation and associations: Toponomic or preservational characteristics in terms of the classification illustrated in Text-Figs. 3.3. and 3.4. The description will also include the type and nature of the host and infilling sediment of the burrow(s). Relationships (e.g., tiering etc.) with other associated trace fossils are also described if they exist.

Ichnofacies and palaeoenvironmental affinities: The general classification of the ichnofacies described in Text-Fig. 3.5 and Table 3.1 are indicated here as a guide in the interpretation of the studied ichnotaxon. The palaeoenvironmental affinities concerned with these ichnofacies are described and discussed in Text-Figs. 5.1, 5.2, and Table 5.1.

CHAPTER 6

LARGE DWELLING-BURROWS

LARGE DWELLING-BURROWS

6.1 INTRODUCTION

In modern times large dwelling-burrows are made by numerous vertebrates and some invertebrates. Familiar vertebrate examples include the burrows of rabbits, moles, certain marsupials (e.g., wombats, bandicoots), certain reptiles (such as lizards), amphibians, some birds, and certain fish (e.g. the lungfish). These burrows can comprise well-defined single tunnels or multiple-tunnel network systems (commonly of considerable complexity), but most consist of temporary passages forced into surface layers of the soil or weathering mantle. Evaluation of the burrowing habits of vertebrates can be made by analyzing the behavior and ecology of modern animals or by examining the functional morphology of their digging appendages; i.e., the function of forelimbs, hindlimbs, and beak or snout (all of which can be used to batter, scrape, or push a tunnel into soil), or by examining the burrow system. The commonest fossil vertebrate burrows are those ascribed to lungfish (Allen & Williams, 1981; and Dubial et al., 1987).

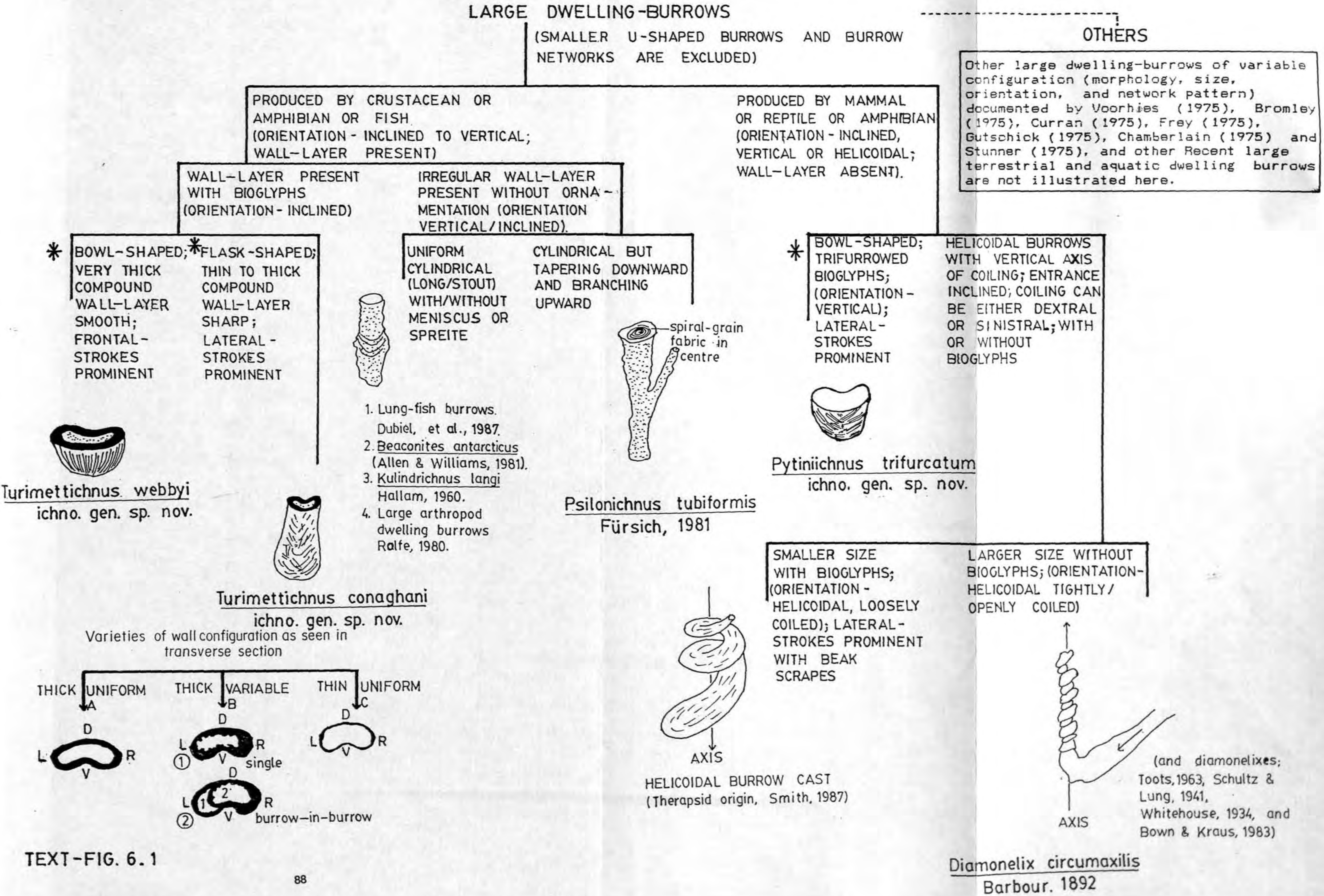
In contrast to the numerous burrows of vertebrates, large dwelling-burrows of invertebrates are few in modern times, but their study follows the same ethological principles as in the case of the vertebrates. Proper scientific classification of these burrows, both modern and ancient, is ultimately necessary for several reasons: firstly, because of the long history of burrowing throughout geological time; secondly, to better understand the analogy between ancient and living forms, together with palaeoenvironmental interpretations; and lastly, to resolve why and how the burrows were made. Fossil burrows provide evidence of unanticipated complex burrowing behavior of organisms (including in some cases, extinct groups of organisms, e.g., Dubial et al., 1987). The morphology of the burrow, the presence/absence of wall-layer(s), and bioglyph patterns on the outer surface of a burrow constitute the most useful characteristic for classifying the large dwelling-burrows. These characteristics also provide important clues about how the burrows were established and used from stage to stage until their abandonment for whatever reason(s).

In environmental terms the burrows of non-aquatic vertebrates are excavated in soil or fluvial deposits by scratching with the feet and also possibly with the beak or snout, and the length/depth of the burrow is probably limited in many cases by the level of the water-table. On the other hand, invertebrate organisms can establish their dwelling-burrows both above the water-table in terrestrial environments and under water in both marine and non-marine aquatic environments.

6.2 THE PROPOSED CLASSIFICATION

The classification proposed here (Text - Fig.6.1) accommodates large burrows (i.e. defined here as burrows of volume in excess of 500 cubic cm), especially those made for dwelling purposes (although some may have been associated also with feeding or other activities), of both vertebrate and invertebrate origin, and established in both terrestrial and marine and non-marine aquatic environments. These types of burrows are

TEXT-FIG. 6.1. Proposed classification for large dwelling-burrows. Other large burrows of various morphologies illustrated by Voorhies (1975), Bromley (1975), Curran (1975), Frey (1975), Gutschick (1975), Chamberlain (1975) and Stunner (1975), and other Recent large dwelling-burrows of both terrestrial and aquatic organisms are excluded here, as are other smaller U-shaped dwelling-burrows and burrow networks. The morphological criteria, genetic relationships and ethological inferences on which the classification is based are detailed in Table 6.2. The prior and revised ichnotaxonomic names of the burrows accommodated in the classification (some of which are figured in this diagram) are given in Table 6.3. Asterisks indicate those burrows that occur in the present study area.



LARGE DWELLING-BURROWS
(SMALLER U-SHAPED BURROWS AND BURROW NETWORKS ARE EXCLUDED)
OTHERS
Other large dwelling-burrows of variable configuration (morphology, size, orientation, and network pattern) documented by Voorhies (1975), Bromley (1975), Curran (1975), Frey (1975), Gutschick (1975), Chamberlain (1975) and Stunner (1975), and other Recent large terrestrial and aquatic dwelling burrows are not illustrated here.
PRODUCED BY CRUSTACEAN OR AMPHIBIAN OR FISH (ORIENTATION - INCLINED TO VERTICAL; WALL-LAYER PRESENT)
PRODUCED BY MAMMAL OR REPTILE OR AMPHIBIAN (ORIENTATION - INCLINED, VERTICAL OR HELICOIDAL; WALL-LAYER ABSENT).
WALL-LAYER PRESENT WITH BIOGLYPHS (ORIENTATION - INCLINED)
IRREGULAR WALL-LAYER PRESENT WITHOUT ORNAMENTATION (ORIENTATION VERTICAL/INCLINED).
* BOWL-SHAPED; VERY THICK COMPOUND WALL-LAYER SMOOTH; FRONTAL-STROKES PROMINENT
* FLASK-SHAPED; THIN TO THICK COMPOUND WALL-LAYER SHARP; LATERAL-STROKES PROMINENT
UNIFORM CYLINDRICAL (LONG/STOUT) WITH/WITHOUT MENISCUS OR SPREITE
CYLINDRICAL BUT TAPERING DOWNWARD AND BRANCHING UPWARD
* BOWL-SHAPED; TRIFURROWED BIOGLYPHS; (ORIENTATION - VERTICAL); LATERAL-STROKES PROMINENT
HELICOIDAL BURROWS WITH VERTICAL AXIS OF COILING; ENTRANCE INCLINED; COILING CAN BE EITHER DEXTRAL OR SINISTRAL; WITH OR WITHOUT BIOGLYPHS
spiral-grain fabric in centre
1. Lung-fish burrows. Dubiel, et al., 1987.
2. Beaconites antarcticus (Allen & Williams, 1981).
3. Kulindrichnus langi Hallam, 1960.
4. Large arthropod dwelling burrows Rolfe, 1980.
Turimettichnus webbyi
ichno. gen. sp. nov.
Turimettichnus conaghani
ichno. gen. sp. nov.
Psilonichnus tubiformis
Fürsich, 1981
Pytiniichnus trifurcatum
ichno. gen. sp. nov.
SMALLER SIZE WITH BIOGLYPHS; (ORIENTATION - HELICOIDAL, LOOSELY COILED); LATERAL-STROKES PROMINENT WITH BEAK SCRAPES
LARGER SIZE WITHOUT BIOGLYPHS; (ORIENTATION - HELICOIDAL TIGHTLY/OPENLY COILED)
Varieties of wall configuration as seen in transverse section
THICK UNIFORM A
THICK VARIABLE B
THIN UNIFORM C
D
L
R
V
① single
② burrow-in-burrow
1
2
AXIS
HELICOIDAL BURROW CAST (Therapsid origin, Smith, 1987)
AXIS
(and diamonelixes; Toots, 1963, Schultz & Lung, 1941, Whitehouse, 1934, and Bown & Kraus, 1983)
Diamonelix circumaxilis
Barbour. 1892

TEXT-FIG. 6.1

very interesting and attractive to ichnologists because some of them are unusually large, and because normally the burrow's morphology, and its internal and external characteristics are readily accessible. However, the main problems lie not so much in their actual study but in their meaningful ethological classification in ichnotaxonomy. Most ichnogenera accommodating large-dwelling burrows in the literature are usually assigned on the basis of their morphology rather than on an ethological basis (Voorhies, 1975). The proposed classification (Text-Fig. 6.1) attempts to understand these large burrows in terms of their detailed ethological meaning by studying their stage-by-stage development, as based largely on two new ichnogenera described herein.

For several reasons, the classification of these large dwelling-burrows is much simpler than is that of the smaller dwelling-burrows: firstly, because they are larger in scale, and the external and internal structure is available together with the overall morphology of the entire burrow or burrow system; secondly, because the skeletal remains of the producing organism can be preserve inside the burrow, especially in the case of vertebrate burrows (cf. Smith, 1987). At the higher level (i.e., at the supra-generic or group level above ichnogenera), the present classification incorporates the taxonomy or biological affinity of the producer organism because this can determine differences in the way that the burrow is made even though the basic reason for making the burrow is or may be the same in the case of each of the different kinds of animals. For example, the

TABLE 6.1. Glossary of terms used in the description and classification of large dwelling-burrows (cf. Text-Fig. 6.1). Terms are emended in some instances.

Large dwelling burrow: Volume of dwelling chamber in excess of 500 cubic cm (cf. Table 6.4).

Bioglyphs: scratch marks on the outer surface of the burrow formed during excavating.

Strokes: individual scratch marks produced by a single movement of forelimbs/arms or hindlimbs/legs or other appendages during digging (see Text-Figs.6.2 & 6.3).

Frontal strokes: strokes produced at the front of the organism on the burrow surface by up-and-down movements of the forelimbs on other frontal appendages/arms.

Lateral strokes: *strokes positioned on the side of the* burrow produced by lateral left-to-right or right-to-left oblique movements of the forelimbs or other frontal appendages (cf. Text-Figs.6.2 & 6.3).

Combination Pattern: Bioglyph pattern formed by the combination or overprinting of individual strokes (see Text-Figs.6.2 & 6.3).

Beak scrapes: broad flat marks developed in front of the organism by its beak or snout, especially in burrows produced by amphibians or reptiles (cf. Smith, 1987).

Bioglyph shape: individual configuration of a scratch mark: e.g., smooth and rounded, sharp and pointed, and smooth and trifurrowed (cf. Text-Fig. 6.11).

Burrow shape: overall shape of a burrow: e.g. cylindrical-shaped (and upward/downward tapering or branching) flask-shaped, bowl-shaped, or coiled.

Helicoidal burrows: coiling trocho-spirally.

Dextral coiling: clockwise coiling when looking down-burrow.

Sinistral coiling: anti-clockwise coiling when looking down-burrow.

Tightly-coiled: spiral whorls are in contact with each other, (closely coiled).

Openly-coiled: spiral whorls are not in contact with each other, (coiling is geometrically regular and is trochospiral).

Loosely-coiled: spiral whorls are not in contact with each other, (coiling is somewhat irregularly but is trochospiral).

Axis: axis of coiling.

Orientation of burrow: inclination of the burrow relative to the plane of bedding or the sediment-water interface.

Orientation of organism: disposition of organism relative to the left/right and dorsal/vertical sides of the burrow (see Text-Figs. 6.2 - 6.4, 6.6 & 6.9).

Anatomical affinities of bioglyphs: forelimb/hindlimb, left/right, frontal, lateral (cf. Text-Figs. 6.2 & 6.3).

Networks: labyrinth-shaped burrow or burrow system (forming an irregularly network).

Entrance: aperture or opening of the burrow.

Terminus: terminal end of the burrow.

Passive fills: burrow filled passively by overlying younger sediment.

Table 6.1. (continued)

Active fills: burrow filled actively by faecal stuff or filled with meniscus or spreite.

Wall(s)/wall–lining/wall–layer(s): structure built for burrow reinforcement or for protection (from predators) or simply for thigmotaxis.

Thick wall: wall thickness more than 0.5 cm.

Thin wall: wall thickness less than 0.5 cm.

Uniform wall: wall thickness uniform throughout the entire burrow.

variable **wall:** wall thickness not uniform throughout the entire burrow.

Section: section cut through burrow exposing internal structures.

Longitudinal section: section cut longitudinally, i.e., parallel to the long axis of the burrow.

Transverse section: section cut transverse to the long axis of the burrow.

Dorsal side (D): outwardly convex side of the burrow (upper side of the burrow during excavation).

Ventral side (V): inwardly convex side of the burrow (lower side of the burrow during excavation).

Right side (R): right-hand side of the burrow (corresponds to the right-hand side of the organism during excavation).

Left side (L): left-hand side of the burrow (corresponds to the left-hand side of the organism during excavation).

Burrow-in-burrow: two generations of burrows established one within the other, or one transecting the other (younger burrow penetrates older).

Spiral grain fabric: spiral type of sediment infill structure in the burrow (cf. Fursich, 1981).

Turn-around: Globose terminus which allows the organism to turn around and face the burrow opening.

nature of the dwelling-burrow will be different depending on whether the producer organism places its home above or below the water-table and this will be a function of its biological affinity.

In the context of devising a hierarchically arranged set of criteria that is designed to allow scientific classification of the burrows at the ichnogeneric and ichnospecific levels, it is difficult to resolve the relative ichnotaxonomic and ethological importance of any particular morphological feature of the burrow, such as for example: burrow shape or geometry, presence/absence of wall-layers, bioglyphs, and other internal structures. One of the main reasons for this difficulty is that it is hard to resolve the separate individual significance of each such feature or characteristic against the contrasting behavioral backgrounds of the different biological or taxonomic groups, beginning with, most importantly, the contrasting behavior of burrowing vertebrates and burrowing invertebrates. Consequently it is inappropriate and hazardous to use and emphasize any one particular morphological feature or characteristic of the burrows and disregard others because while that feature or characteristic may have major ethological significance in the burrows of some animals it may be of only minor significance in the burrows of others. For the purposes of the proposed classification a hierarchically arranged set of morphological and genetic criteria and ethological inferences focused separately at the different ichnotaxonomic levels (i.e., supra-generic, generic and specific and variety levels) has been formulated (Table 6.2). It is difficult to evaluate the relative merits of these criteria

Table 6.2. Morphological criteria and characteristics and ethological inferences used in the classification of large dwelling burrows (cf. Text-Fig.6.1). The order of listing of the various criteria within each of the major categories of criteria in this tabulation is not meant to imply in this tabulation is not meant to imply their order of relative significance or importance. Rather, the criteria within each major category should be regarded as of equal importance. See text for further discussion.

I. Significant features (group level)

(1) Taxonomic or biological affinity of the producer. e.g. crustacean, amphibian, reptile, fish, or unknown producer in unusual-shaped burrows.

(2) Ethology - burrow mainly used for dwelling (other ethological purposes subsidiary).

II. Major accessory features (generic level)

(1) Orientation of burrow. Axis of burrow inclined, vertical, or horizontal; coiling either dextral or sinistral.

(2) Burrow dimensions (size of burrow). Length, width, diameter, volume of burrow, volume of living chamber, and living chamber to burrow volume ratio.

(3) Shape of burrow. Flask-shaped, bowl-shaped, cylindrical-shaped, spiral-shaped, labyrinthine networks, (Coiling either open, loose, tight).

(4) Shape of transverse cross-sections. e.g. dorsal-ventral asymmetry (reniform-shaped), or circular sub-circular, or elliptical or other shapes.

(5) Presence/absence of bioglyphs.

(6) Presence/absence of wall layer(s).

III. Accessory features (specific level)

(1) Presence/absence of surface ornamentation (i.e., bioglyphs).
(a) Types of bioglyphs.
e.g. Lateral strokes (left and/or right), frontal strokes, beak scrapes (in the case of amphibian or reptiles), and combination patterns.
(b) Shapes of bioglyphs.
e.g. smooth, rounded/wide, sharp/narrow, and single, or multifurrowed (e.g., trifurrowed).

Table 6.2. (continued)

(2) Genetic nature and structure of infilling sediment.
(a) Type of infills (passive or active).
(b) Faecal stuff or non-faecal sediment.
(c) Presence/absence of spreite or meniscus.
(d) Special types of structures e.g. spiral grain fabric.

IV. Minor accessory features (used only for differentiation of informal form-varieties).

Thickness and uniformity of thickness of wall layer in transverse section.
(1) Thick, uniform.
(2) Thick, variable (single burrow or burrow-in-burrow).
(3) Thin, uniform.

and inferences but their general importance in this context should be obvious and self-explanatory.

In approaching the classification of any particular large dwelling-burrow using the classification scheme proposed here (cf. Text-Fig.6.1) and the various criteria on which the scheme is based (Table 6.2), it is necessary and important to subjectively evaluate the likely significance of each criterion to that particular burrow, beginning, naturally, with the criteria termed "significant" and proceeding down through the hierarchy of "major accessory", "accessory", etc. This step of subjective evaluation is particularly important at the supra-generic or group level since the "significant" criteria advocated in Table 6.2 to be appropriate at this step are: (1) the biological on taxonomic affinity of the producer organism; and (2) the ethological reason(s) for which the burrow was made. Clearly, the evaluation of the questions posed by each of these criteria is to a very large degree subjective, and dependent upon the ichnotaxonomical and relevant biological experience and breadth of understanding of the investigator. Contrastingly, the "major accessory" and "accessory" criteria emphasize morphological features that are judged to be of value to the ethological interpretation rather than to the systematics or taxonomy of the producer organism and are somewhat more straightforward in their application.

Any approach to classification that involves the stratigraphic age of the form-taxa is judged here not to be appropriate. Also excluded from the proposed classification are some of the large dwelling-burrows with variable morphology illustrated by Vorhies (1975), Bromley (1975), Curran (1975), Frey (1975), Gutschick (1975) and suttner (1975). The proposed classification as illustrated in Text-Fig. 6.1 focuses primarily on fossil burrows from ancient rocks rather than modern examples. Numerous other large dwelling-burrows of modern and sub-Recent/Pleistocene aquatic and terrestrial animals are not incorporated into the proposed classification as depicted in Text-Fig. 6.1 because extension of the classification in this way is beyond the scope of the present project. The smaller U-shaped and cylindrical-shaped dwelling-burrows will be discussed in other chapters.

A number of terms are employed in describing and classifying large dwelling-burrows and the meaning of such terms is given in Table 6.1. The need for this terminology stems primarily from the fact that, notwithstanding the common purpose for which the burrow was made, a large number of biologically different organisms are involved in making such burrows and this is reflected in their morphological diversity and mode of construction.

The proposed classification scheme deals with two major groups of burrows (Text-Fig. 6.1): to first group belong flask-shaped, bowl-shaped, and cylindrical-shaped burrows produced by crustaceans, fish and amphibians, mainly for dwelling. Within this group there are four major subdivisions at the generic level. The first is Turimettichnus webbyi which is bowl-shaped, mud-lined, and characterized by prominent frontal-stroke bioglyphs. The second ichnogenus is Turimettichnus conaghani (the type ichnogenus of this group), a flask-shaped mud-lined dwelling-burrow with marked dorso-ventral asymmetry and with prominent lateral-stroke bioglyphs. The third ichnogeneric category contains several previously described and differently named cylindrical burrows some of which were probably produced by lungfish. The fourth ichnogeneric category includes the ichnogenus Psilonichnus tubiformis Fürsich, 1981, which is cylindrical, but tapers downwards and branches upwards, with an internally spiral arrangement of grain fabric.

The second major group contains two major subgroups: the first subgroup contains the new ichnogenus Pytiniichnus trifurcatum, which is a medium-sized bowl-shaped burrow characterized by smooth lateral trifurrowed bioglyphs produced almost certainly by an amphibian or an amphibian-like reptile. The second major subgroup contains previously described large helicoidal burrows, with or without bioglyphs and wall-layer(s) (cf. Text-Fig. 6.1). These latter burrows were produced by mammalian-like reptiles or mammals.

The proposed classification is mainly based on the two new ichnogenera Turimettichnus (probably produced by a large crustacean), and Pytiniichnus (produced by an amphibian or an amphibian-like reptile). The discovery of a large crustacean body fossil associated with a burrow of T. conaghani (Plate 74, Figs. a & b) and the association of the smaller crustacean burrows Ophiomorpha and Thalassinoides with it support the notion that the new ichnogenus Turimettichnus conaghani is of crustacean origin.. The other species of this new genus, Turimettichnus webbyi has a thick wall-layer (like many specimens of T. Conagha-

Table 6.3. Details of large dwelling-burrows and large burrows suspected of being dwelling-burrows accommodated in the proposed classification (cf. Text-Fig.6.1). The burrows depicted include some from the present study area and some from the literature[1].

Ethology	Producer	Size and morphology of burrow	Original/ previous name	Proposed scientific name
(1) Dwelling permanent	Crustacean	Large flask-shaped, marked dorso-ventral asymmetry; thick or thin wall-layer with prominent bioglyphs; sharp/narrow lateral strokes predominent.	(New ichnogenus)	<u>Turimettichnus conaghani</u>
(2) Dwelling semi-permanent	?Crustacean	Large bowl-shaped, subdued dorso-ventral asymmetry; thick wall-layer with prominent bioglyphs; smooth frontal stroke bioglyphs prominent.	(New ichnogenus)	<u>Turimettichnus webbyi</u>
(3) Dwelling	Amphibian or reptile	Medium sized, bowl-shaped, marked dorso-ventral asymmetry; wall-layer absent; smooth/ wide trifurrowed lateral stroke bioglyphs prominent.	(New ichnogenus)	<u>Pytiniichnus trifurcatum</u>
(4) Dwelling & Feeding	Lungfish	Medium to large sized, cylindrical-shaped, vertical to inclined; irregular wall-layer present; bioglyphs absent.	Lungfish burrow Dubial et al., 1987	none yet proposed

Table 6.3 (continued)

Ethology	Producer	Size and morphology of burrow	Original/ previous name	Proposed scientific name
(5) Dwelling & Feeding	Lungfish? or worm or lizard or blind snake	Medium to large sized, cylindrical-shaped, vertically orientated but inclined in some parts; wall-layer absent, but internal meniscus and spreite present.	<u>Beaconites antarcticus</u> Allen & Williams, 1981	<u>Beaconites antarcticus</u> Allen & Williams, 1981
(6) Estivation	Lungfish?	Medium to small sized, stumpy cylindrical burrow with rounded base and phosphatic wall-layer.	<u>Kulindrichnus langi</u> Hallam, 1960	<u>Kulindrichnus langi</u> Hallam, 1960
(7) Dwelling & crawling	Arthropod ?	Not adequately described.	Unnamed Ralfe, 1969	Unnamed
(8) Dwelling	Crustacean	Medium sized, cylindrical-shaped burrow, tapering downwards and branching upwards, with internal spiral grain fabric.	<u>Psilonichnus tubiformis</u> Fürsich, 1981	<u>Psilonichnus tubiformis</u> Fürsich, 1981
(9) Dwelling	Mammalian-like reptile	Medium sized, spiral-shaped burrow with open dextral coiling and with irregular bioglyphs.	Helicoidal burrow cast	<u>Diamonelix</u> Barbour, 1892 (but probably of different species)

Table 6.3 (continued)

Ethology	Producer	Size and morphology of burrow	Original/ previous name	Proposed scientific name
(10) Dwelling	Beaver (rodent)	Large sized helicoidal-shaped (tight dextral or sinistral) without bioglyphs.	*Diamonelix circumaxilis* (Barbour, 1892)	*Diamonelix circumaxilis* Babour, 1892; (& Toots, 1963; Schultz, , 1942; Whitehouse, 1934; and Bown & Kraus, 1983)

1. Excluded from this table are large dwelling-burrows mentioned and illustrated by Voorhies (1975), Bromley (1975), Curran (1975), Frey (1975), Gutschick (1975), Stunner (1975), Chamberlain (1975), and other Recent large dewlling-burrows from non-marine and marine areas (see Text-Fig. 6.1).

ni) but has a different shaped burrow and different bioglyph pattern (prominent frontal-strokes). Its producing organism still remains unknown but because of the similarity of the burrow's shape and construction with that of T. conaghani the producing organism is also thought to have been a crustacean. The type species T. conaghani can be divided into three varieties on the basis of the thickness and pattern of development of the wall-layer as seen in transverse cross-sections (cf. Text-Fig. 6.1). The other new ichnogenus P. trifurcatum has distinctive trifurrowed bioglyphs that were almost certainly produced by an amphibian or an amphibian-like reptile (see Text-Figs. 6.8 & 6.9, Plate 5, Fig. d). A summary of the characteristics of the burrows accommodated in the scheme of Text-Fig. 6.1 is given in Table 6.3, together with known or inferred producing animals, the ethological purpose of the burrow, and previous and proposed revised names of the burrows.

6.3. SYSTEMATIC ICHNOTAXONOMY

Ichnogenus Turimettichnus ichno. gen. nov.

Derivation of names: `Turimett' from the Turimetta Head locality in the Sydney Northshore area (Text-Figs. 1.2 & 1.3 ) and `ichnus' from Greek `iknos', meaning trace.

Diagnosis (generic assignment): Large mud-lined flask- or bowl-shaped burrows, with surface of burrow ornamented with well-defined bioglyphs (scratch marks).

Remarks (diagnostic features): Large flask- to bowl-shaped burrows with dorso-ventral asymmetry (reniform-shape) in transverse cross-section, lined by a thick compound wall-layer; burrow surface ornamentated with single-line (i.e., monofurrowed) bioglyphs.

Taxonomic keys for generic assignment:

(1) Fairly large subcylindrical flask- to bowl-shaped structures whose long axes are inclined (commonly at a steep angle) to bedding; burrows are not coiled (cf. Smith, 1987).

(2) Endichnial burrow cast (cf. Martinsson, 1970) or endogene cast (full-relief) (cf. Seilacher, 1953).

(3) Large hollow living-chamber (dwelling-chamber occupies 50% to 70% of the overall burrow; see Table 6.4).

(4) Not interconnected with other burrows (but commonly associated with other smaller crustacean burrows).

(5) Thick compound wall-layer present: comprising, from the outside-in, layers **A**, **B**, and **C**; the aggregate thickness of these layers can be as much as 2.5 cm or as little as 1 cm or less, and the thickness either uniform or variable throughout the burrow (cf. Text-Fig. 6.1).

(6) Very distinct bioglyph pattern on the surface of the burrow, either consisting of a bilaterally-arranged single-line system of narrow furrows or a system of smooth unidirectional single-line furrows (cf. Text-Fig. 6.11).

(7) The middle wall-layer **(B)** is the thickest and is of homogeneous mud.

(8) Locally and only in some specimens, a thin innermost carbonaceous wall-layer (layer **C**).

Ichnospecies (type) T. conaghani ichno. sp. nov.

Plate 1, Figs. a - e (holotype)
2, Figs. a - c "
3, Figs. a - d (paratype)

4, Figs. a - d "
5, Figs. a - b (holotype)
6, Figs. a - d (holotype)
7, Fig. a "
Fig. c
8, Figs. a - c (paratype)
9, Figs. a - c
10, Figs. a - c
11, Figs. a - b
12, Figs. a - b
13, Figs. a - o
14, Figs. a - p

Derivation of the name: Named for Dr. P. J. Conaghan of the School of Earth Sciences, Macquarie University.

Diagnosis (specific assignment): A large flask-shaped burrow with strong dorso-ventral asymmetry in transverse cross-section, lined by a variously thick or thin compound wall-layer; burrow surface is ornamented with distinct bilaterally-arranged narrow monofurrowed bioglyphs.

Remarks (diagnostic features): Flask-shaped, variously thick or thin compound wall-layer with bilaterally-arranged narrow bioglyphs.

Description and ethology:

(1) Appearance and dimensions: Turimettichnus is reconstructed as an elongated hollow cylindrical, bulbous-, flask- or bottle-shaped structure with a thick compound mud wall-lining or wall-layer and, as viewed from the outside of the burrows, with a broad median depression on the ventral side (Text-Fig. 6.4A; Plate 1 Fig.d, Plate 2 Figs.b & c, Plate 3 Figs.b & d). The wide apertural opening or entrance for the organism is at the top end (Text-Fig. 6.3; Plate 2 Fig. 6, Plate 4 Figs. b - d). The base of the burrow is somewhat inflated, or bulbous, but is not large enough to be described as a turn-around (Text-Figs. 6.3 & 6.4B;

Plate 1, Plate 2 Fig.c, Plate 3 Figs. a & b). Laterally the burrow has two sides: the ventral side of the burrow is convex inwards and the dorsal is convex outwards (Text-Fig. 6.4A; Plate 2 Figs. b & c) as a consequence of the predominant orientation of the animal during excavation (Text-Figs. 6.4, and 6.5 substages 1 to 3). The long axis of the burrow varies from being very steep to shallowly-inclined to the bedding (Plate 6, Plate 7 Fig.c, Plate 8), the maximum inclination observed being 70°. The common presence of slickensides on the burrow surface (Plate 1 Figs. d & e, Plate 2 Fig. a, Plate 5 Fig.a) indicates slight differential movement between the heavy infilled-burrow and its host sedimentary surrounds, but such movement was probably minor and may not have involved much vertical rotation. If rotational movement in the vertical plane did occur, its effect would likely have been to steepen rather than reduce the angle of inclination.

Detailed measurements of the burrows (Table 6.4) were used to calculate the 'dwelling ratio', i.e. the proportion of the volume of the total excavation used for dwelling following the construction of the wall-lining by the organism; in the holotype specimen the length of the burrow is 26 cm, the width is 8 cm and the breadth is 13 cm (Text-Fig. 6.3); the thickness of the compound wall-layer is 1.4 cm and is almost uniform throughout the burrow. The living or dwelling ratio is calculated from the formula:

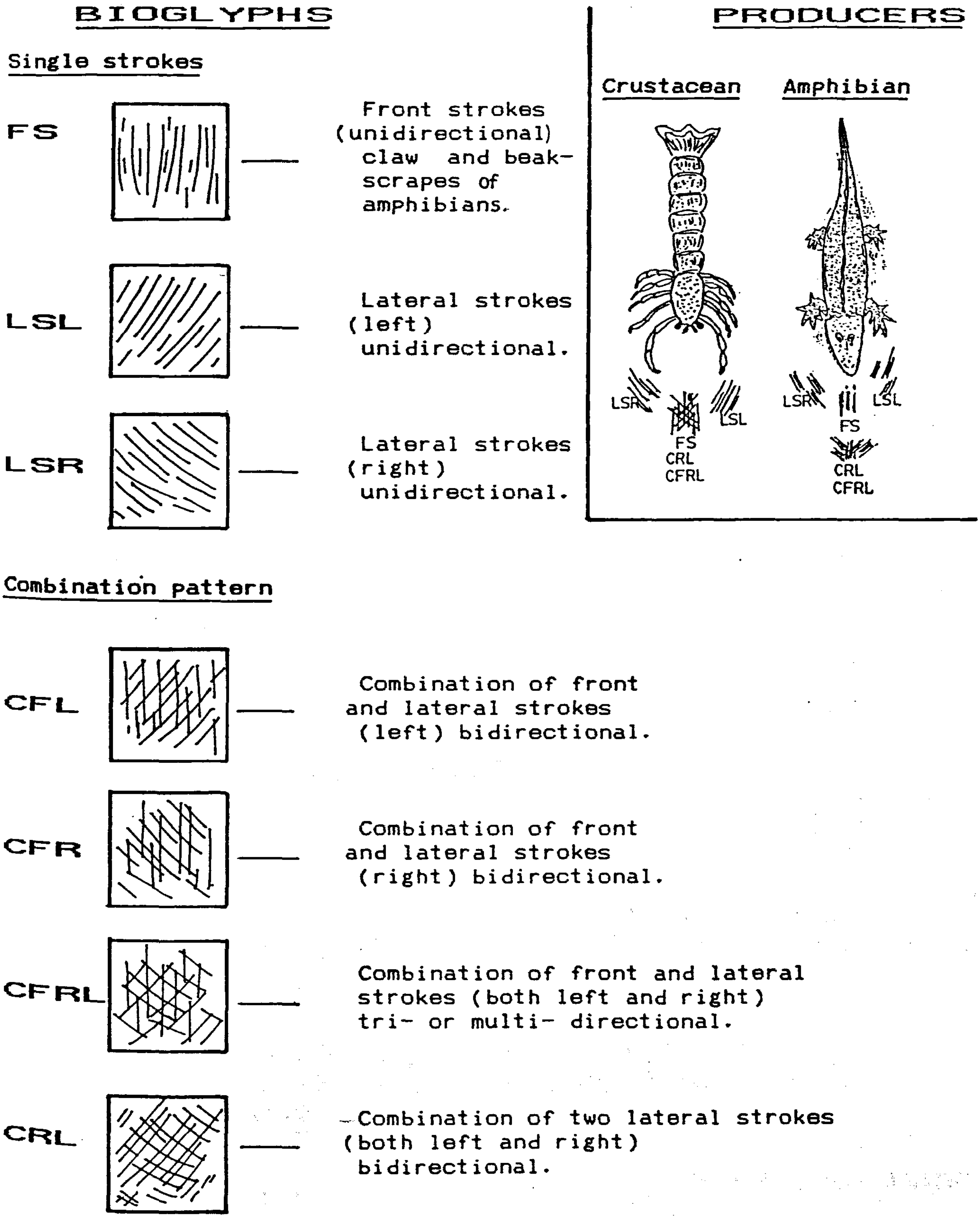
$$\text{Dwelling ratio (\%)} = \frac{\text{volume of animal living chamber}}{\text{total volume of excavation}} \times 100$$

The total volume occupied by the organism for dwelling is 48% of the total burrow excavation in the case of the holotype specimen (Table 6.4). Generally half the volume (50%) of the entire burrow excavation is occupied by the dwelling-chamber in T. conaghani and more than half (60%) in the case of T. webbyi (Table 6.1). There are also many problematic cases where the burrow is not fully exposed (e.g. Plate 7 Figs.b & d, and Plates 13 & 14) and hence where it is not possible to accurately reconstruct the original dimensions, particular the length. Nevertheless, in this situation the exposed part of the burrow (commonly transverse cross-sections, cf. Plates 13 & 14) can be used to estimate the dwelling ratio. Providing the wall-layer of the burrow is uniform in thickness, the dwelling ratio can be assessed to correspond approximately to the ratio of the area of the dwelling-chamber to the area of the entire burrow as seen in transverse cross-section (cf. Text-Fig.6.4A; Table 6.4, data regarding "T. conaghani?").

There are two major burrow characteristic that control the value of the ratio of the dwelling-chamber of the animal to that of its entire burrow excavation: these are firstly the shape-uniformity of the burrow and, secondly, the thickness-uniformity of the compound wall-layer. Only an approximate value of the dwelling ratio can be made in the case of irregular-shaped burrows and also in burrows with variable wall-layer thickness.

(2) The bioglyph patterns and their interpretation: The bioglyphs (scratch or digging marks) are distinctive markings on the outer surface of the burrows (Text-Figs. 6.3, 6.4 & 6.11A & B; Plate 1, Plate 2 Fig.a, Plate 3, Plate 5 Fig.a, and Plate 6). These bioglyphs show recognizably different stroke movements of the organism's appendages: two lateral-strokes and a frontal-stroke

TEXT-FIG. 6.2. Interpretation of bioglyph patterns produced by stroke movements of organisms during the excavation of dwelling-burrows. Although this interpretation may have general validity to a number of different taxa it is here based on and illustrated with references to a decapod crustacean and on amphibian, the organisms believed to have been responsible for the new ichnogenera Turimettichnus conaghani and Pytiniichnus.


BIOGLYPHS
PRODUCERS
Single strokes
FS
Front strokes (unidirectional) claw and beak- scrapes of amphibians.
LSL
Lateral strokes (left) unidirectional.
LSR
Lateral strokes (right) unidirectional.
Crustacean
Amphibian
LSR
LSL
FS
CRL
CFRL
Combination pattern
CFL
Combination of front and lateral strokes (left) bidirectional.
CFR
Combination of front and lateral strokes (right) bidirectional.
CFRL
Combination of front and lateral strokes (both left and right) tri- or multi- directional.
CRL
Combination of two lateral strokes (both left and right) bidirectional.

TEXT-FIG. 6.2.

TEXT-FIG. 6.3. Oblique dorsal view side-view of the holotype specimen of T.conaghani showing the various bioglyphs patterns on the outermost surface of wall-layer **A**. These patterns can be interpreted and named by reconstructing the position of the inferred producer organism shown at top in the burrow and the relevant excavation movements made in that position.

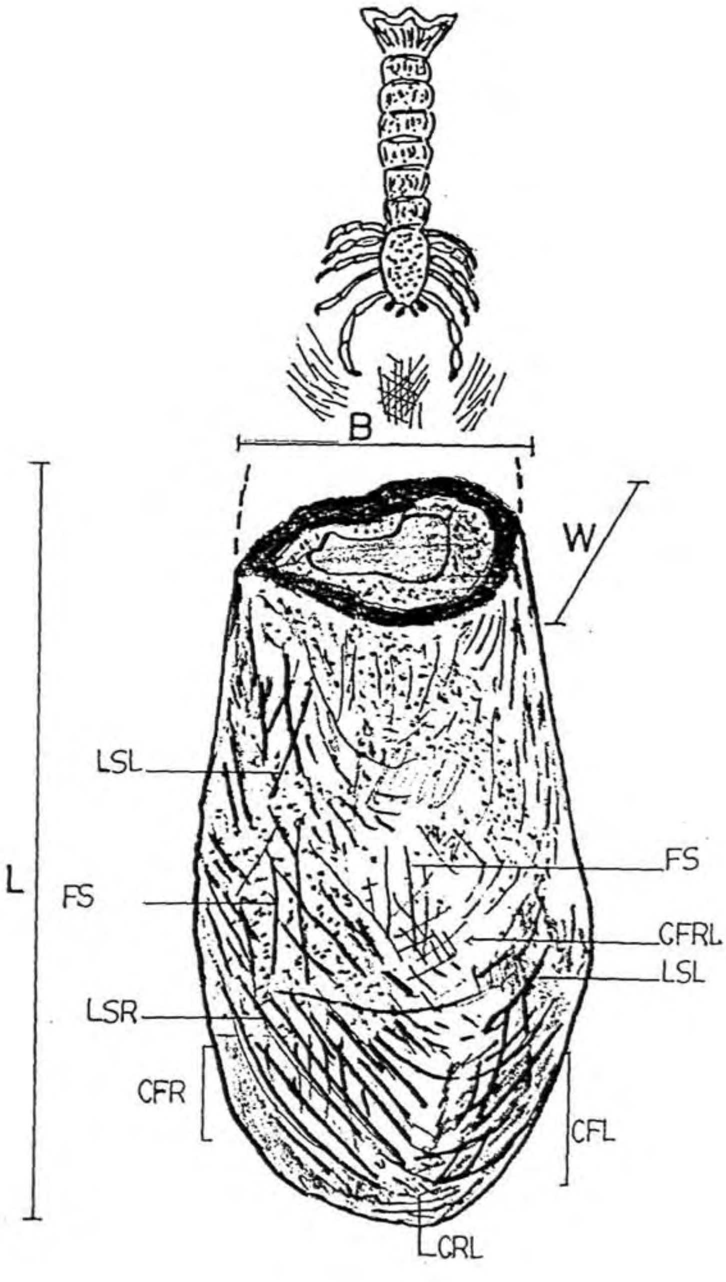
Seven different patterns of animal behaviour can be interpreted from the three types of scratch marks (see also Text-Fig. 1.2).

(a) Pattern **FS**, **LSR** and **LSL** are unidirectional patterns made by the organism only where and when it was in a stationary position.

(b) Pattern **CFR** and **CFL** are combination pattern made by the organism while it was in motion, either digging downwards or enlarging the burrow laterally.

(c) Pattern **CFRL** is a combination pattern made by the organism while it was in motion reworking a previously worked surface.

(d) Pattern **CRL** is a combination pattern made by the organism while it was in motion. This pattern is mainly found in the bottom of the burrow and in the lateral wall where it respectively manifests the downward extension of the burrow and the widening of the burrow on surface that have been previously worked on.



L - LENGTH = 26 cm.

W - WIDTH = 8 cm.

B - BREADTH = 13 cm.

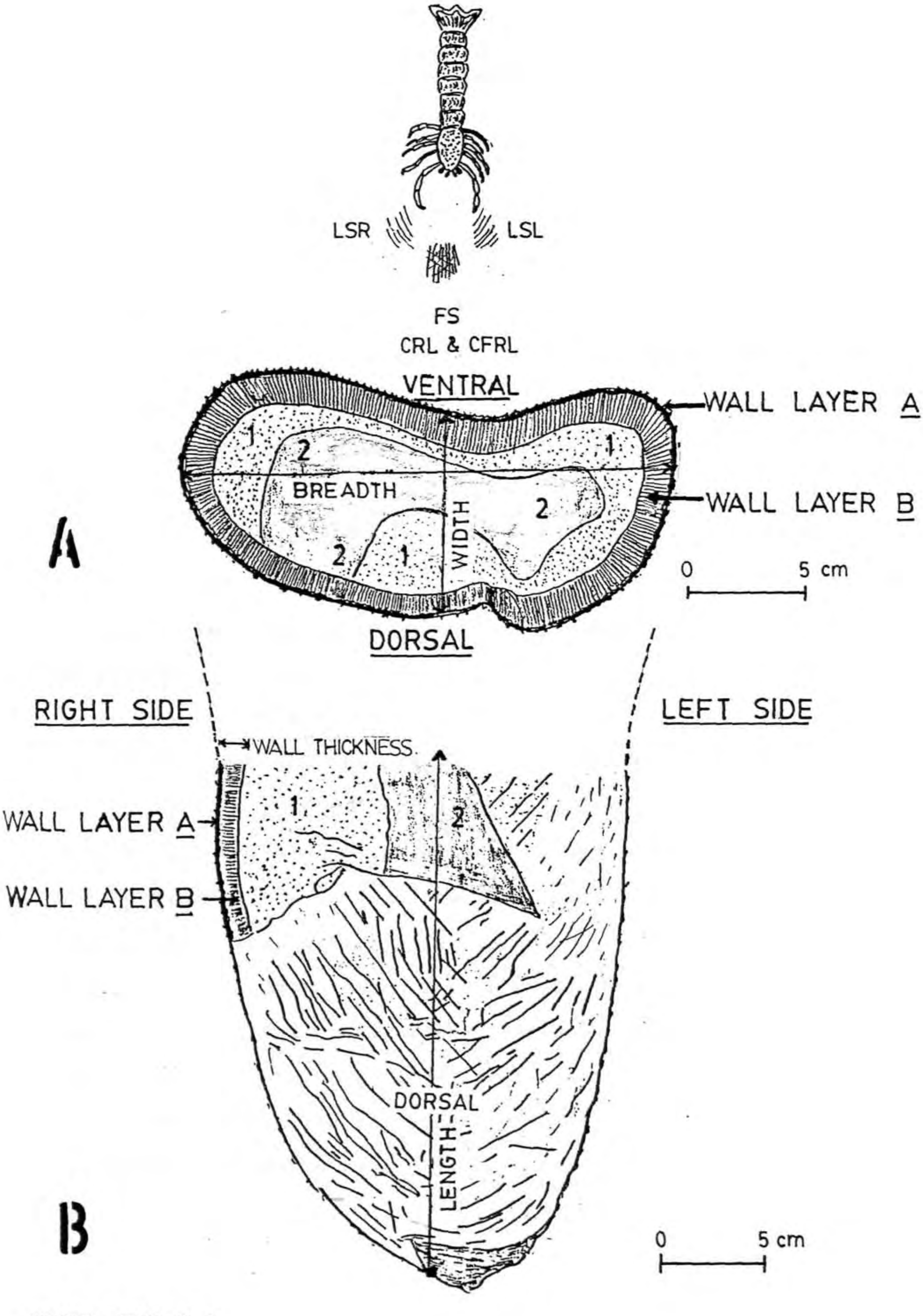
WALL THICKNESS = 1.4 cm.

TEXT-FIG. 6.3.

(Text-Figs. 6.2 & 6.3). These patterns manifest the animal's digging movements during the final stages of excavation and also reflect the orientation of the organism within the burrow during that particular stage (Text-Fig. 6.5). They can be grouped into two major strokes (Text-Figs. 6.2 & 6.3): vertical strokes made in front of the producer organism and termed frontal-strokes (FS); and inclined or oblique strokes made on each side of the producer organism and termed lateral-strokes (LS). The lateral-strokes comprise both left (LSL) and right (LSR) ones corresponding to the orientation of the organism. The frontal-strokes are almost vertical or steeply-inclined and are very shallowly impressed (Text-Fig. 6.3; Plate 2 Fig.a). The lateral-stroke movements are deeply impressed, are inclined about 45° to the horizontal (Plate 2 Fig.a, Plate 3, Plate 5 Figs.a & b, Plate 6), and appear to have been relatively more effective than the frontal-strokes in the excavation process. The organism is believed to have excavated its burrow with its head in a downward position and with its underside facing the ventral side of the burrow most of the time while digging (Text-Figs. 6.3 - 6.5; see also Plate 14 Fig.b).

The superimposition of these three stroke movements (FS, LSL, and LSR) over time resulted in an intersecting criss-cross pattern on the surface of the burrow (Text-Figs. 6.2 & 6.3). This resulted in four combination stroke patterns (Text-Fig. 6.2): (1) combination of frontal-strokes (FS) and left-lateral-strokes (LSL) called **CFL**; (2) combination of frontal-strokes (FS) and right-lateral-strokes (LSR) called **CFR**; (3)

TEXT-FIG. 6.4. Turimettichnus conaghani shown in apertural view (A) and dorsal side-view (B), together with the reconstructed inferred producer organism shown in digging orientation (with bioglyphs) relative to the burrow. Size of the reconstructed producer organism is not necessarily accurate relative to the size of the burrow. Details of the burrow are based on the holotype specimen (cf. Plate 1 Fig, a, Plate 2 Fig. b, Plate 6, and Plate 7 Fig.a). The reconstructed producer organism is based in part on the poorly-preserved crustacean body fossil shown in Plate 74 Figs. a and b. Note strong dorso-ventral asymmetry of burrow as seen in apertural view and thick compound wall-lining. Stratigraphy of passively infilled sediments is: 1 - very fine sand (= first infilling layer); 2 - mud (second infilling layer).


LSR
LSL
FS
CRL & CFRL
VENTRAL
WALL LAYER A
WALL LAYER B
BREADTH
WIDTH
1
2
A
0
5 cm
DORSAL
RIGHT SIDE
LEFT SIDE
WALL THICKNESS
WALL LAYER A
WALL LAYER B
DORSAL
LENGTH
B
0
5 cm

TEXT-FIG. 6.4.

combination of frontal-strokes (FS) with both left- and right-lateral-strokes (LSL and LSR) called **CFRL**; (4) combination only of left- and right- lateral-strokes (LSL and LSR) called **CRL.** These four combination patterns are distributed on the burrow's surface as a result of the animal's location and orientation within the burrow and movements of the animal's limbs (see Text-Fig. 6.3). The CFL pattern is located on the left-hand side of the burrow and the CFR pattern is located on the right-hand side of the burrow. The CFRL and CRL patterns, characterized by criss-crossing strokes, are normally located on the middle part of the dorsal side or on the basal part of the burrow, and manifest the reworking of previously worked surfaces. All these bioglyph patterns are preferentially developed on the dorsal side rather than on the ventral side of the burrow (Text-Fig. 6.3).

(3) Excavation of the burrows, formation of the compound wall-layer and ethological interpretation:

The excavation of the burrow, formation of the different wall-layers and the ethological interpretation are illustrated in Text-Fig. 6.5. There are four recognizable stages in the formation of the burrow. Before the excavation process begins, the organism has to find the most suitable place or the right ecological conditions. These conditions might include substrate types, water temperature, salinity, food supply, absence of competition, relationship with other organisms, etc. Most crustaceans have a planktonic larval stage (Maginite, 1934; Phol, 1946; and many others) and subsequently enter a settlement phase that is usually triggered by a physico-chemical stimilus. The organism

TEXT-FIG. 6.5. Interpretative diagram of developmental stages of the new ichnotaxon <u>Turimettichnus conaghani</u> based on details of the holotype specimen. Four major stages can be reconstructed in the development of the burrow. These stages followed site selection by the organism on a suitable substrate. The boxes labelled **A** show median longitudinal cross-sections of the developing burrow and those labelled **B** show apertural views of the same. Other details of the diagrams are explained in the legend below. Note that the vertical cross-sections of the burrow are somewhat schematic inasmuch as the vertical exaggeration is x2.

The stages of the burrow's development are as follows (arrows in substages 1 to 3 indicate the animal's orientation with respect to the burrow during excavation):

I. Stage of excavation

(1) Initial substage of excavation.
(2) Intermediate substage of excavation.
(3) Final substage of excavation.

II. Stage of wall construction.

(4) Substage of construction of wall-layer **A** (thin layer preserving the bioglyphs).
(5) Substage of construction of wall-layer **B** thick layer).

III. Stage of permanent occupation.

(6) Substage of permanent occupation of burrow and establishment of a very thin inside wall-layer (layer C; used for farming?, breeding or other purposes?).

IV. Stage of abandonment.

(7) Burrow is partially filled by very fine sand (layer 1) (because of changes in physical conditions) and the ecology becomes hostile to the organism.
(8) Burrow is totally filled by mud (layer 2). By this stage the organism has already relocated to another more suitable place.

EXPLANATION

(Text. Fig. 6.5)

A Longitudinal cross-section of the burrow in the host sediment.

B Top view of transverse section of the burrow in the host sediment.

D Dorsal side.

V Ventral side.

L Left side.

R Right side.

1 Infilled sediment layer 1 (very fine sand).

2 Infilled sediment layer 2 (mud).

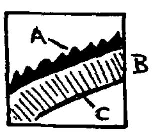
1-8 Stages of burrow development.

↑ Orientation of the organism during excavation (stages 1 - 3 in the series of diagrams showing apertural views).

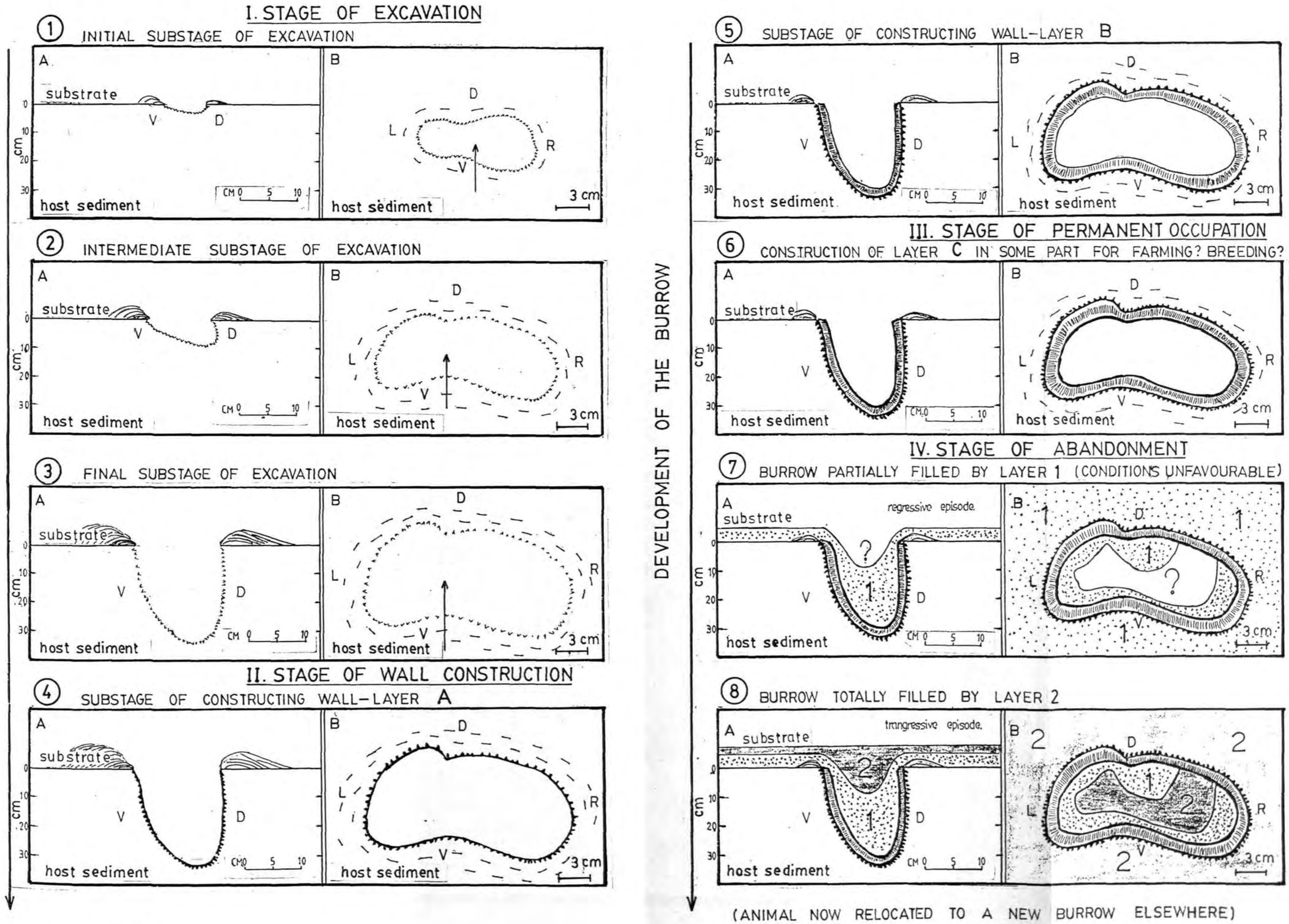
? Presence of organism uncertain.

Excavated sediment around the burrow aperture in the cross-sectional views.

Excavated sediment around the burrow aperture in the series of diagrams showing apertural views.



Wall-layers A, B and C, with bioglyphs.


DEVELOPMENT OF THE BURROW
I. STAGE OF EXCAVATION
① INITIAL SUBSTAGE OF EXCAVATION
② INTERMEDIATE SUBSTAGE OF EXCAVATION
③ FINAL SUBSTAGE OF EXCAVATION
II. STAGE OF WALL CONSTRUCTION
④ SUBSTAGE OF CONSTRUCTING WALL-LAYER A
⑤ SUBSTAGE OF CONSTRUCTING WALL-LAYER B
III. STAGE OF PERMANENT OCCUPATION
⑥ CONSTRUCTION OF LAYER C IN SOME PART FOR FARMING? BREEDING?
IV. STAGE OF ABANDONMENT
⑦ BURROW PARTIALLY FILLED BY LAYER 1 (CONDITIONS UNFAVOURABLE)
⑧ BURROW TOTALLY FILLED BY LAYER 2
A
B
substrate
host sediment
V
D
L
R
cm
0
10
20
30
CM 0 5 10
3 cm
regressive episode
trangressive episode
?
1
2
(ANIMAL NOW RELOCATED TO A NEW BURROW ELSEWHERE)

TEXT-FIG. 6.5.

then starts the first stage of the excavation (Text-Fig. 6.5, substage 1). During the following substages of the excavation the organism must maintain the most efficient position to harvest suspended food from the prevailing bottom currents. The long axis of the inclined burrow (i.e., dimension "L" in Text-Fig. 6.3) was probably aligned in the current and at right angles to the shore-line rather than at random, analogous to such patterns documented for the burrows of modern crustaceans by Allen & Curran (1974), Chakrabarti (1981) and others. The excavation stage is an important one in the animal's life history (and burrow history) and its duration has a bearing on the structure and durability of the burrow. Most modern crustaceans are deposit-feeders while they are in the excavation stage and become suspension-feeders when semi-permanently or permanently occupying their burrows (Dworkschak, 1983).

At a certain stage in the excavation (in substage 3 of the excavation stage in Text-Fig. 6.5) when the burrow is large enough to accommodate the producer organism, it stops excavation and starts the process of building a peripheral wall of mud (cf. Swinbanks & Luternauer, 1987). The wall-layer serves to strengthen and reinforce the fairly large hollow of the excavation in the soft clayey host sediment and, being impervious, might also aid or enhance thigmotaxis behavior. The wall-layer is constructed only after the organism has gone through the semi-permanent or permanent dwelling stage.

The first stage of construction of the wall-lining involves the construction of wall-layer **A** which is important because it is the layer that preserves the bioglyphs present at the final stage of excavation. These bioglyphs are the most important ichnotaxonomic characteristic of the ichnogenus. Layer **A** is very thin, less than 2 mm in thickness, and, by analogy with modern crustaceans, is made up of clay particles cemented with mucus produced by the organism (Dworschak, 1983; and reference therein). This layer is dark brick-red or dark-brown in colour and is readily distinguishable from the surrounding host sediment (Plate 7). The nature of the contact with the surrounding sediment is sharp and irregular because of the bioglyphs (see Text-Fig. 6.4A). The purpose of layer **A** (which is impervious) is to seal off the burrow from the surrounding host sediment. The internal contact of layer **A** with the second wall-lining, layer **B**, is either diffuse or sharp and commonly irregular (Plate 2 Fig.b, Plate 4 Figs.b & c, and Plate 7).

Layer **B** is the thickest layer (average thickness: 1.3 cm) comprises homogeneous mud, and is darker in colour than layer **A** (see last-mentioned plates). Layer **B** serves as a support or reinforcement for the burrow, which is likely to collapse at any time in the soft clayey substrate. This layer is comparable with the mud lining in <u>Ophiomorpha</u> (Frey et al., 1978) and is seen in some modern crustacean burrows (Phol, 1946; Ohsima, 1967; Shinn, 1968; Braithwaite & Talbot, 1972; Farrow, 1971; Ott et al., 1976; Djores, 1978; and Swinbanks & Luternauer, 1987).

The third or innermost wall-lining, layer **C**, is a dark carbonaceous layer but was observed only in some specimens. It is a very thin layer and is discernible only on certain parts of the inner surface of layer **B**. It is likely that its purpose was for farming or for breeding as with many modern crustaceans (Dworschak, 1983). This layer was formed only after the completion of layer B and is believed to have been established only during the semi-permanent or permanent occupation stage.

The organism may have continued to dwell in the burrow or to temporarily vacate it or possibly abandon it because of unfavorable changes in the physico-chemical environment or because of other disturbance (Text-Fig. 6.5, substages 7 and 8). The location of the burrow may have started to shoal or to become locally inundated with storm deposits and consequently the burrow become partially infilled with sediment (cf. deposit 1 comprising very fine-grained sand in the holotype specimen). Subsequent changes resulted in more sediment infilling (deposit 2 comprising clays in the holotype specimen). After this stage it would have been impossible for the organism to dwell in the burrow because it was almost entirely filled.

No remains of the organism that likely made these burrows or any of the organism's faecal stuff have been found inside the burrows. However, at one place at Long Reef Point, a large poorly-preserved crustacean body fossil was discovered on a rock platform associated with and possibly within a burrow (see Plate 74, Figs. a & b, and Text-Fig.16.1).

<u>(4) Possible producer and associated burrows:</u> <u>Turimettichnus conaghani</u> is believed to have been produced by a crustacean or crustacean-like organism for dwelling purposes (domichnia, Seilacher, 1953). The kind of producer organism can be deduced from four features of the burrows themselves. Firstly, the distinctive

bioglyphs are patterns that can only have been produced by an organism with sharp appendages; secondly, the burrows are associated with other kinds of burrows that are widely believed to relate to crustaceans (i.e., Ophiomorpha and Thalassinoides); thirdly, the burrows have a thick peripheral lining of mud as in some modern crustacean burrows (e.g. Ophiomorpha; Phol, 1946; Ohsima, 1967; Shinn, 1968; Braithwaite & Talbot, 1972; Farrow, 1971; Ott et al., 1976; Pemberton, 1976; Djores, 1987; and Swinbanks & Luternauer, 1987); and fourthly, as mentioned above, one decapod crustacean body fossil (of a size appropriate for the burrows) was discovered associated with burrows (Plate 14 Figs. a & b; Text-Fig. 16.2). These features provide strong evidence that T. Conaghani results from the activity of a crustacean, most probably a moderately large decapod crustacean, but not the same crustacean responsible for the ichnogenera Ophiomorpha and Thalassinoides because of the smaller size of the latter. The organism responsible for T. conaghani was very likely larger than the organism that produced Ophiomorpha and Thalassinoides. The crustacean organism that was responsible for T. conaghani used them for dwelling as in the case of many modern crustaceans (Weimer & Hoyt, 1964). No in situ animal remains have been found in the burrows of Turimettichnus, but, as mentioned above, a large decapod crustacean body fossil was found associated with the burrows at Long Reef Point. The recent discovery in the USA (Hasiotis & Mitchell, 1989) of a decapod crustacean fossil inside a similar large dwelling-burrow previously thought to have been produced by a lungfish (Dubiel et al., 1987) confirms the present interpretation of a crustacean origin for the large dwelling-burrows described here. Several other records of crustacean body fossils in the Triassic of the Sydney Basin exist (e.g., Chilton (1928) and numerous crustacean body fossils have been recorded from the late Palaeozoic of eastern Australia (cf. Moore, 1962 p.R353). The incompletely recorded history of the decapod crustaceans extend back to the Devonian (Schram et al., 1978).

Comparison: Other trace fossils produced by crustaceans (cf. Chamberlain & Baer, 1973) are not strictly comparable with the new ichnogenus. Although many trace fossils have bioglyphs on the surface of the burrow (e.g., Rhizocorallium, Spongeliomorpha, Strophichnus, etc.) the shape of the burrow and the bioglyph pattern developed in T. conaghani are totally different (see Text-Figs. 6.2 - 6.4, 6.11A & B). Although the irregular-shaped bioglyphs present in the `helical burrow casts' of Smith (1987) are partly comparable with those of T. conaghani, other characteristics of these two dwelling-burrows are not. Firstly, Smith's helicoidal burrow casts have broad ridge-like bioglyphs that are parallel to the long axis of the burrow and which he interpreted as "beak scrapes". (cf. `frontal-strokes' in the present study - see Text-Fig.6.2). In contrast the frontal-stroke marks in T. conaghani are very shallow and are only just discernible (Plate 2 Fig.a). Secondly, unlike T. conaghani, Smith's helicoidal burrow casts lack a wall-lining of any kind. Thirdly, the shape of the helicoidal burrow is conspicuously different to T. conaghani (Text-Fig.6.1). And lastly and most importantly, Smith's helicoidal burrows were made by a theraspid mammal-like reptile that lived and excavated its burrows in terrestrial environments.

Studied material: Numerous specimens of T. conaghani have been discovered at Turimetta Head, Long Reef Point, and St. Michaels Cave. Several specimens were collected from the field and have been curated in the Earth Sciences Collection, Macquarie University. Holotype specimen: 212/MU.44351; paratypes: 213/MU.44352, 216/MU.44354, 2096/MU.44355, and 306/MU.44367.

Distribution: Numerous specimens of T. conaghani occur at Turimetta Head (area 2) and Long Reef Point (area 3), at both places within trace fossil subintervals IC1-5 of the Bald Hill Claystone (see logged sections 2.1.1 and 2.2.1 measured at Turimetta Head). T. conaghani was later found to also occur in the St. Michaels Cave area (area 5) in the upper part of the Lower Newport Member, i.e., in trace fossil subinterval ID1. No Turimettichnus burrows have been found in the Middle and Upper Newport Members.

Preservation and association: T. conaghani burrows are invariably preserved as full-relief endichnial forms. Turimettichnus burrows are associated with the other crustacean burrows Ophiomorpha and Thalassinoides in trace fossil subintervals IC1-5 of the Bald Hill Claystone exposed at Turimetta Head, and are associated with Skolithos and Rhizocorallium in trace fossil subinterval ID1 of the Lower Newport Member exposed at St. Michaels Cave.

Ichnofacies and palaeoenvironmental affinities: T. conaghani belongs to the Skolithos ichnofacies and is associated with Ophiomorpha, Thalassinoides, Skolithos, and Rhizocorallium. On this basis its environmental affinities can be interpreted as brackish-marine to intertidal shallow-marine.

Varieties: Turimettichnus conaghani can be divided into three varieties on the basis of the thickness and configuration of wall-layer B (Text-Fig. 6.1).

<u>T. conaghani</u> **var. A**

Plate 1 Figs. a - e
2 Figs. a - c
4 Fig. d
6 Figs. a - d
7 Figs. a - c
8 Figs. a - c

Diagnosis (varietal assignment): Medium to large flask-shaped burrow with a thick uniform wall-layer (layer B) throughout.

Description (and association): The holotype specimen of <u>Turimettichnus</u> belongs to the var. A category. These burrows are well preserved with dorso-ventral asymmetry in transverse cross-section (i.e., reinform shape) and with well-defined bioglyphs. <u>T. conaghani</u> var. A is confined to trace fossil subintervals IC3-4 of the Bald Hill Claystone at Turimetta Head and Long Reef. In the former locality it is associated with <u>Ophiomorpha</u> and <u>Thalassinoides</u> but at Long Reef it occurs without association with any other burrows.

<u>T. conaghani</u> **var. B**

Plate 3 Figs. a - d
4 Figs. a - c
7 Figs. b & d

Diagnosis (varietal assignment): Medium to large flask- to cylindrical-shaped burrows with irregular and variable thickness of wall-layer B throughout the burrow (cf. Text-Fig.6.1).

Description (and association): <u>T. conaghani</u> var. B is normally associated with var. A in trace fossil subintervals IC3-4 of the Bald Hill Claystone at Turimetta Head. However, the variety B structures are normally not very well preserved, are more cylindrical-shaped rather than flask-shaped, and with weaker dorso-ventral asymmetry in transverse cross-section. They are readily recognized by the uneven thickness of wall-layer **B** in transverse cross-sections. The association of T. conaghani varieties A and B is confined to trace fossil subintervals IC3-4 of the Bald Hill Claystone at Turimetta Head where they are both associated with Ophiomorpha and Thalassiniodes.

T. conaghani var. C

Plate 9 Figs. a - c
Plate 10 Figs. a - c
Plate 11 Figs. a & b
Plate 12 Figs. a & b
Plate 13 Figs. a - o
Plate 14 Figs. a - p

Diagnosis (varietal assignment): Medium size, flask-shaped with thin uniform wall-layer (possibly layer **A** only; wall-layer is poorly defined in all specimens so that layers **A** and **B** are difficult to differentiate), present throughout the burrow structure (Text-Fig.6.1).

Description (and association): T. conaghani var. C is not associated with var. A and var. B. Variety C is only known from trace fossil subinterval ID1 of the Lower Newport Member exposed in the St. Michaels Cave area (area 5). Although the burrows are preserved as full-relief forms they are only exposed as transverse cross-sections on rock platforms. They exhibit strong dorsoventral asymmetry. The bioglyphs are not well exposed so as to permit resolution of particular stroke movements of the animal. Where it occurs within trace fossil subinterval ID1 of the Lower Newport Member at St. Michaels Cave T. conaghani var. C is associated with Skolithos and Rhizocorallium.

Ichnospecies <u>T. webbyi</u> ichno. sp. nov.

Plate 15, Figs. a - d (holotype)
Plate 16, Figs. a & b "
Fig. c (paratype)

Derivation of name: Named for Associate Professor B. D. Webby of the Department of Geology and Geophysics, the University of Sydney.

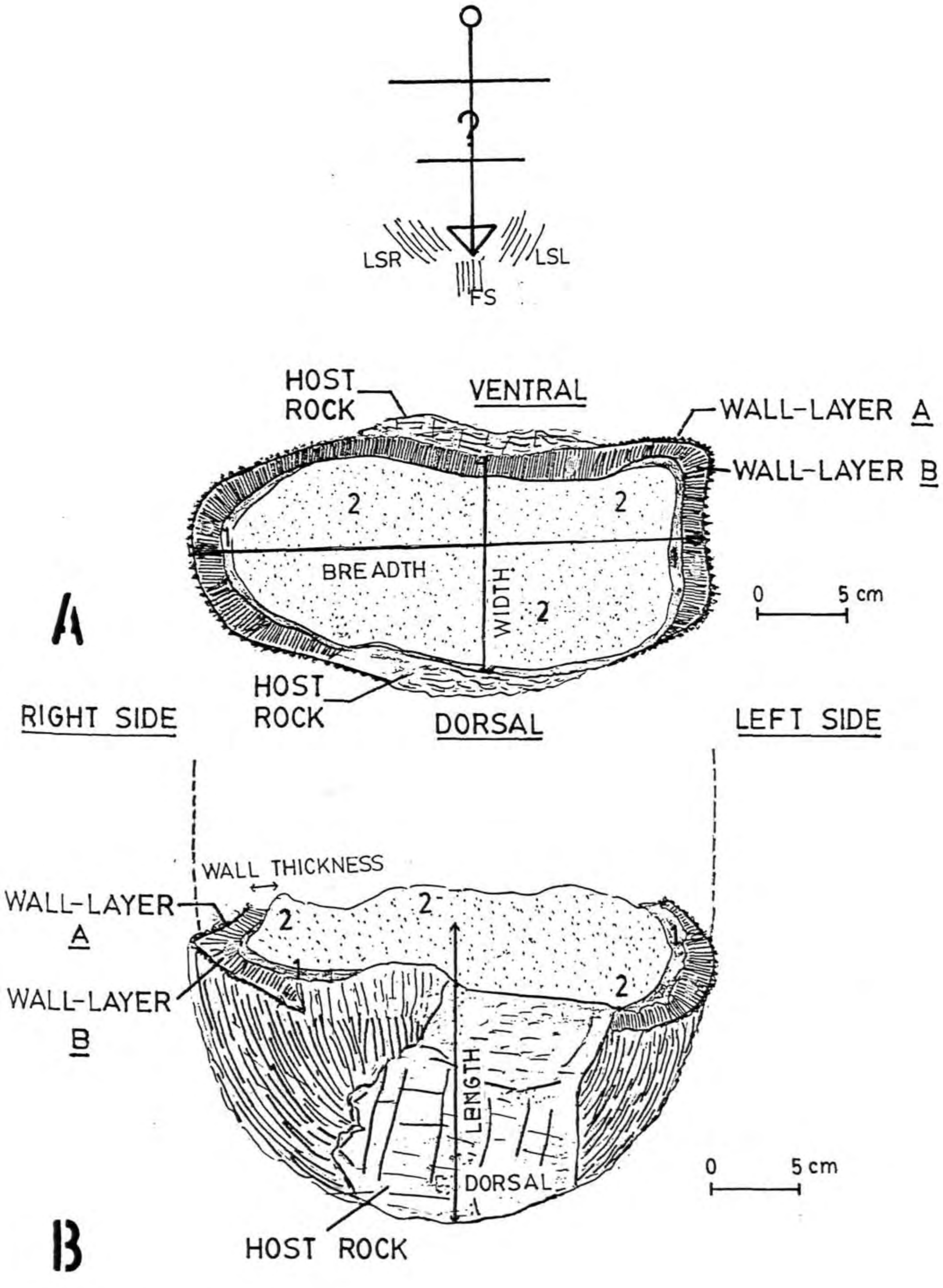
Diagnosis (specific assignment): Large bowl-shaped burrow with weak dorso-ventral asymmetry in transverse cross-section; the burrow is lined by a very thick compound wall-layer ornamented with distinct smooth monofurrowed bioglyphs produced exclusively by frontal-stroke movements.

Remarks (diagnostic features): Large bowl-shaped burrow with very thick compound wall-layer, the burrow surface being ornamented with smooth unilaterally-arranged monofurrowed bioglyphs.

Description (and ethology):

<u>(1) Appearance and dimensions:</u> This species is more globose in shape than the flask- and cylindrical-shaped type species (Text-Figs.6.1 & 6.6; Plates 15 & 16). By comparison the aggregate thickness of the wall-layers is 2.5 cm (cf. 1.5 cm in the type species; Table 6.4), and the dwelling ratio is 64% (compared to an average of 50% in <u>T. conaghani</u>) reflecting a larger dwelling-chamber (details follow) and the necessity of a stronger wall-layer for better reinforcement of the overall structure. Thus strengthened (Plate 15 Fig.b, Plate 16 Figs.a & b), the burrow is believed to have been more durable than that of the type species. The wider aperture would have been beneficial for easier food gathering from suspended particles (if the organism was indeed a suspension-feeder), but it would have made the organism more

TEXT-FIG. 6.6. Turimettichnus webbyi shown in apertural view (A) and oblique dorsal view (B), together with the reconstructed orientation of its unknown (but probable crustacean) producer organism shown in digging orientation (with bioglyphs) relative to the burrow. Reconstructed size of the producer organism is not necessarily accurate relative to the size of the burrow. Diagrams of burrow are based on details of the holotype specimen (cf. Plates 15 & 16). Note weak dorso-ventral asymmetry in diagram **A**. Stratigraphy of passive sediment infills is: **1** - mud (first infilling layer; **2** - fine sand (second infilling layer).


?
LSR
LSL
FS
A
HOST ROCK
VENTRAL
WALL-LAYER A
WALL-LAYER B
2
2
BREADTH
WIDTH
2
0
5 cm
HOST ROCK
RIGHT SIDE
DORSAL
LEFT SIDE
WALL THICKNESS
WALL-LAYER A
WALL-LAYER B
2
2
1
1
2
LENGTH
DORSAL
0
5 cm
B
HOST ROCK

TEXT-FIG. 6.6.

exposed to attack by predators. Possibly, this type of burrow served as a hiding place from predators or as a semi-permanent dwelling. The base of the burrow is more rounded and globose than in the type species (Text-Fig. 6.6B, Plate 16), and is characterized by weak dorso-ventral asymmetry in transverse cross-section (Text-Fig. 6-6A, Plate 15 Fig.b).

The length of the holotype burrow is 17 cm, the width is 14 cm and the breadth is 26 cm (Table 6.4). The total volume of the burrow is almost 6200 cubic cm (twice that of the holotype specimen of T. conaghani var. A but slightly smaller than one of the paratype burrows of T. conaghani var. B (Table 6.4); and the total volume occupied by the organism for dwelling is 3198 cubic cm (64%). The dwelling ratio or capacity of the dwelling varies as a function of the size and shape of the burrow and thickness of the compound wall-layer (see Table 6.4). It is also related to the size and shape of the inhabitant producer organism and may also reflect ethological differences as well.

(2) The bioglyphs and their interpretation: The bioglyph pattern is simple in contrast to that of the type species (Text-Figs. 6.6B & 6.11C & D; Plate 15 Fig.a, Plate 16, Figs.a & b). The pattern resulted from a series of vertical to steeply-inclined frontal-stroke movements (FS) produced by the appendages/fore-limbs of the inhabitant (evidently resulting in the production of just one groove per stroke; Text-Fig.6.11C & D). The pattern suggests the likelihood of a more rapid excavation than in the case T. conaghani, and this is further indicated by the shallow nature of the burrow and its wider opening. Whether the burrow

TEXT-FIG. 6.7. Interpretative diagram of developmental stages of the new ichnotaxon <u>Turimettichnus webbyi</u>. Four major stages can be reconstructed in the development of the burrow represented by the holotype specimen (cf. Plates 15 & 16). These stages followed site selection by the organism on a suitable substrate. Other details of the diagrams are as for Text-Fig. 6.5. Vertical and horizontal scales are the same in this figure.

The development of the burrow can be reconstructed as follows:

I. Stage of excavation.

(1) Initial substage of excavation.
(2) Intermediate substage of excavation.
(3) Final substage of excavation.

II. Stage of wall construction.

(4) Substage of construction of wall-layer A (thin layer preserving the bioglyphs).
(5) Substage of construction of wall-layer B (thick mud layer).

III. Stage of permanent occupation.

(6) Substage of permanent occupation (no evidence of layer C , hence use of burrows for farming and breeding activities is unclear).
(7) Burrow is partially filled by mud (layer 1) mainly in the base.

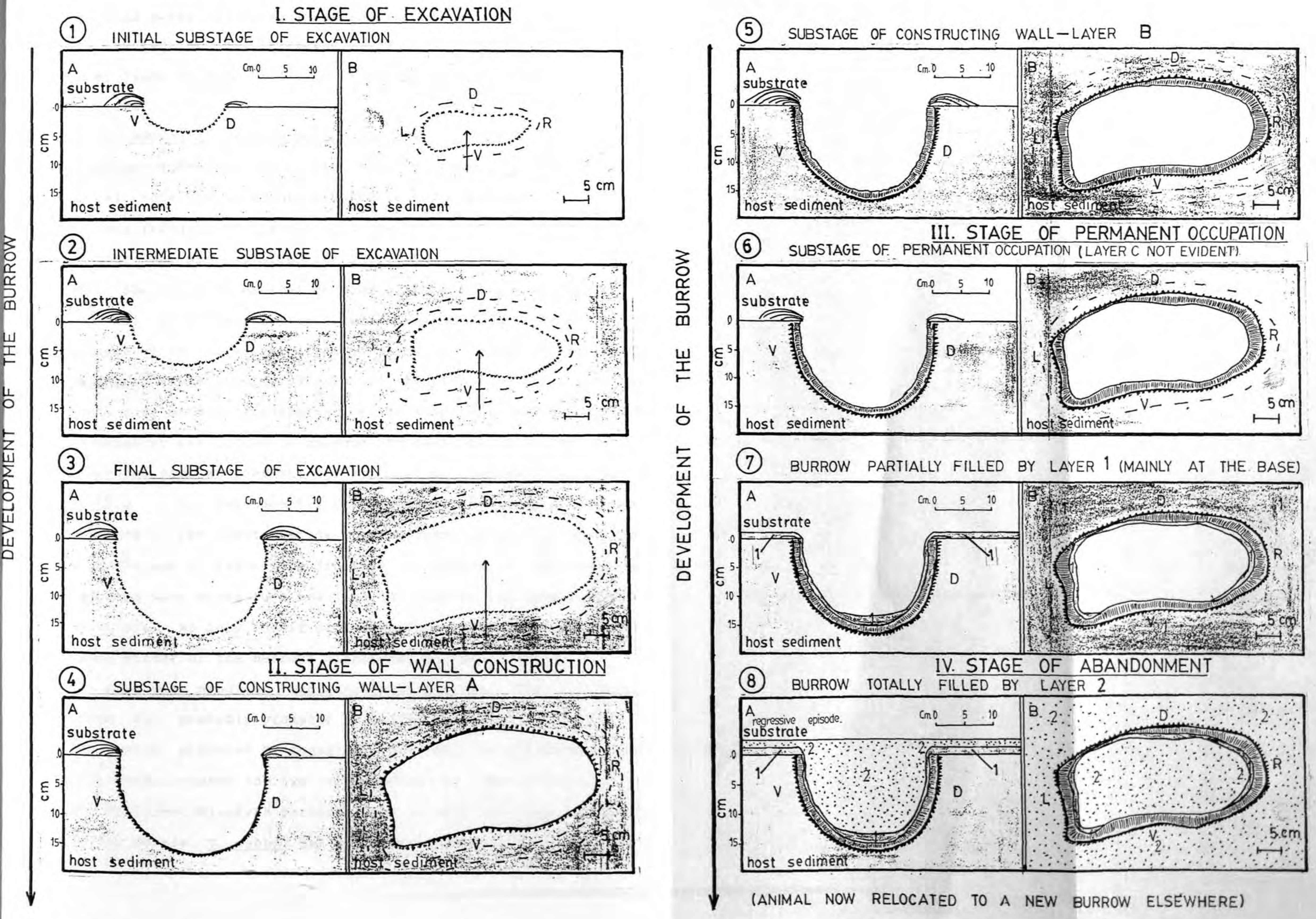
IV. Stage of abandonment.

(8) Burrow is totally filled by very fine sand (layer 2). By this stage the inhabitant organism has already relocated to a more suitable place.

EXPLANATION

(Text-Fig. 6.7)

A	Longitudinal cross-section of the burrow in the host sediment.
B	Top view of transverse section of the burrow in the host sediment.
D	Dorsal side.
V	Ventral side.
L	Left side.
R	Right side.
1	Infilled sediment layer 1 (mud).
2	Infilled sediment layer 2 (very fine sand).
1-8	Stages of burrow development.
↑	Orientation of the organism during excavation (stages 1 - 3 in the series of diagrams showing apertural views).
?	Presence of organism uncertain.
	Excavated sediment around the burrow aperture in the cross-sectional views.
	Excavated sediment around the burrow aperture in series of diagrams showing apertural views.
	Wall-layers A, B and C, with bioglyphs.



I. STAGE OF EXCAVATION
1 INITIAL SUBSTAGE OF EXCAVATION
2 INTERMEDIATE SUBSTAGE OF EXCAVATION
3 FINAL SUBSTAGE OF EXCAVATION
II. STAGE OF WALL CONSTRUCTION
4 SUBSTAGE OF CONSTRUCTING WALL-LAYER A
5 SUBSTAGE OF CONSTRUCTING WALL-LAYER B
III. STAGE OF PERMANENT OCCUPATION
6 SUBSTAGE OF PERMANENT OCCUPATION (LAYER C NOT EVIDENT)
7 BURROW PARTIALLY FILLED BY LAYER 1 (MAINLY AT THE BASE)
IV. STAGE OF ABANDONMENT
8 BURROW TOTALLY FILLED BY LAYER 2
A
B
substrate
host sediment
regressive episode.
V
D
L
R
Cm 0 5 10
5 cm
cm
DEVELOPMENT OF THE BURROW
(ANIMAL NOW RELOCATED TO A NEW BURROW ELSEWHERE)

TEXT-FIG. 6.7

was used permanently, semi-permanently or temporarily is difficult to resolve. The thick wall-layers (Text-Fig. 6.6; Plate 15 Fig.b, Plate 16 Figs. a & c) contributed to the durability of the structure.

<u>(3) Formation of the compound wall-layer and ethological interpretation:</u> The formation of the compound wall-layer and the ethological interpretation are illustrated in Text-Fig. 6.7. There are four recognizable phases of animal behavior in the construction of the burrow. After the animal had selected a suitable site, the stage of excavation took place and was followed by a phase of wall construction (layer **A** and layer **B**). There is no evidence of an equivalent layer to the layer **C** that occurs in <u>T. conaghani</u>. The organism followed the same dwelling activities as in the case of the type species. After some time in the dwelling the organism was forced to abandon the basal parts of the burrow because of partial sediment infilling (i.e., sediment layer **1** in Text-Fig. 6.7, substage 7). Subsequently, additional sediment infilling of the entire burrow (cf. sediment layer 2 in Text-Fig. 6.7 substage 8) forced the organism to abandon it. The organism must then have moved to a new site and started the same procedure as before. No body fossil of the producer organism is evident inside either of the burrows discovered so far.

<u>(4) Possible producer and associated burrows:</u> The <u>T. webbyi</u> burrow was probably produced by a similar type of organism to that which produced <u>T. conaghani</u>, possibly a crustacean. The differences between the two ichnospecies are, most significantly, the different bioglyph patterns, and in part the size and shape of the burrow. <u>T. webbyi</u> has a thicker aggregate wall (2.5 cm),

the layers (i.e. layers A and B) are clearly discernible (Plate 15 Fig.b) and their individual thickness is uniform throughout the entire structure. Unlike in T. conaghani, wall layer C is not evident. T. webbyi is associated with the type species T. conaghani (paratypes) and the burrows of other crustaceans (i.e. Ophiomorpha and Thalassinoides.

Comparison: No other trace fossil is strictly comparable with this new ichnospecies in terms of shape, size and very distinctive bioglyph pattern.

Studied material: At the present stage of study only two specimens have been discovered; the holotype specimen (209a/MU.44356; shown in Plate 15, Figs. a - d, and in Plate 16, Figs. a & b) was collected from Turimetta Head (area 2) and the other (paratype) specimen from Bilgola Head (area 10a; this specimen is shown in Plate 16, Fig. c and has not been retrieved from the field).

Distribution: The holotype specimen was discovered in trace fossil subinterval IC2 of the Bald Hill Claystone at Turimetta Head (area 2) and the paratype specimen was discovered in trace fossil subinterval ID1 of the Lower Newport Member at Bilgola Head (area 10a).

Preservation and association: The holotype specimen is preserved as a full-relief form in trace fossil subinterval IC2 where it was associated with Ophiomorpha, Thalassinoides, and fossil pellets (produced by crustaceans). The paratype specimen is also preserved as a full-relief form and where it occurs in trace fossil subinterval ID1 of the Lower Newport Member it is associated with packed burrows of Skolithos.

Ichnofacies and palaeoenvironmental affinities: *T. webbyi* belongs to the *Skolithos* ichnofacies, and on the basis of its association with *Ophiomorpha*, *Thalassinoides*, and *Skolithos* its environmental affinities can be interpreted as brackish-marine to intertidal shallow-marine.

Ichnogenus *Pytiniichnus* Ichno. gen. nov.

Derivation of name: `Pytine' from Greek meaning flask covered with plaited work, and `ichnus' from Greek `iknos' meaning trace.

Diagnosis (generic assignment): Burrows produced by an amphibian or amphibian-like reptile, distinguished by their bilaterally-arranged trifurrowed lateral-stroke bioglyphs.

Remarks (diagnostic features): Medium-sized bowl-shaped burrow with strong dorso-ventral asymmetrical (reniform) shape in transverse cross-section, without protecting wall-layer; outer surface of the burrow is ornamented with bilaterally-arranged trifurrowed lateral-stroke bioglyphs.

Taxonomic keys:

(1) Medium-sized bowl-shaped burrow (unlike the helicoidal burrow shape described by Smith, 1987).

(2) No wall-layer is evident.

(3) The inhabitant occupied almost 100% of the excavation (i.e., dwelling ratio almost 100%; cf. Table 6.4).

(4) Trifurrowed lateral-stroke bioglyphs characterize the burrow surface (cf. Text-Figs. 6.8 & 6.11E & F).

(5) The burrow was probably excavated by an amphibian or an amphibian-like reptile, and was established in a subaerial habitat (i.e. above the ground-water-table).

(6) No globose or inflated turn-around feature is present; the organism evidently entered the burrow by forward movements in a head-downward position and exited the burrow in the same orientation by backward movements (cf. Text-Fig. 6.10).

(7) The burrow is not associated with other burrows of the same or any other kind.

Ichnospecies **P. trifurcatum ichno. sp. nov.**

Plate 17, Figs. a & b
Plate 18, Figs. a & b

Derivation of name: 'tri' meaning triple, and 'furcatum' meaning furrow (meaning triple-line furrow or trifurrowed bioglyph).

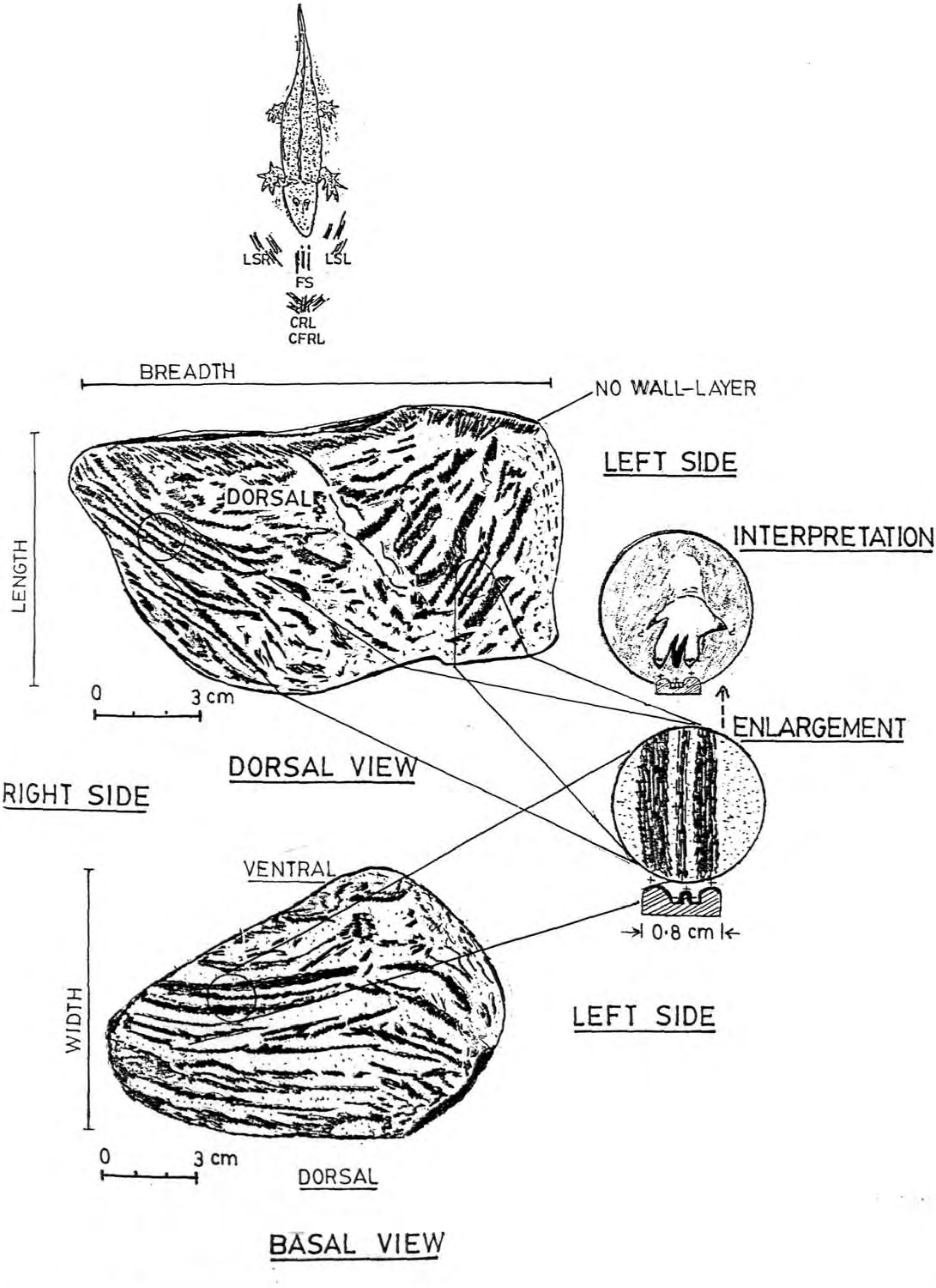
Diagnosis (specific assignment): Bilaterally arranged trifurrowed bioglyphs (manifesting lateral-stroke movements).

Remarks (diagnostic features): (As in ichnogenus).

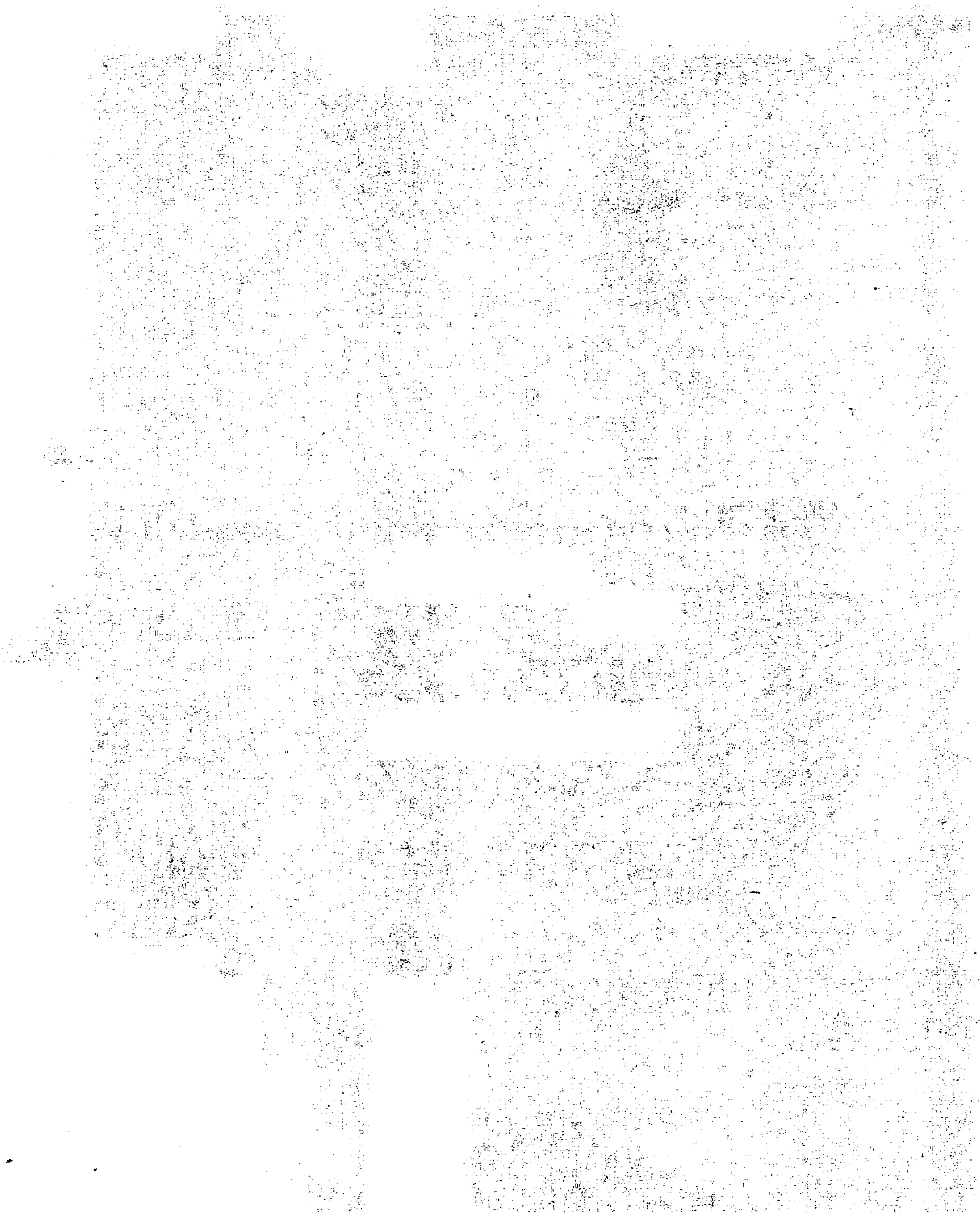
Description and ethology:

(1) Appearance and dimensions: Pytiniichnus trifurcatum is a medium-sized bowl-shaped burrow whose long axis is inclined at about 45° to bedding and hence to the sediment palaeosurface (Text-Fig. 6.10A). As viewed from the outside of the burrow the ventral surface is characterized by a broad median depression (i.e. it is convex inwards) and the dorsal surface is convex outwards. Hence, in transverse cross-section the burrow shows dorso-ventral asymmetry. Only one specimen of P. trifurcatum has been located to date and this is a composite structure consisting of a younger burrow (burrow 2) truncating an older burrow (burrow 1) (Plate 17, Figs. a & b; and Plate 18 Fig. b). However, the specimen is incompletely preserved so that the original length of the burrows can not be measured (see Table 6.4). For the two

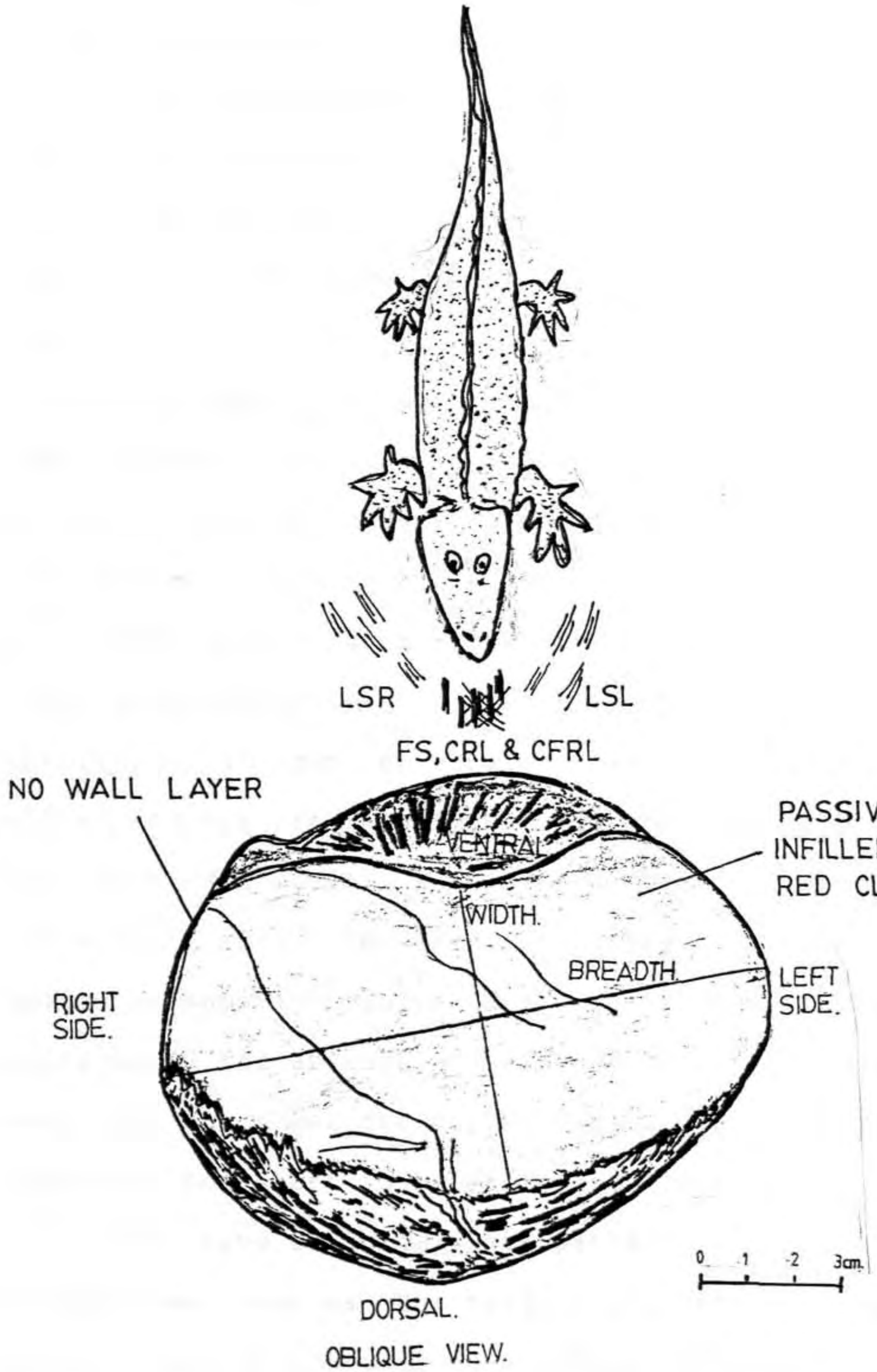
TEXT-FIG. 6.8. Dorsal and basal views of the holotype specimen of the new ichnotaxon Pytiniichnus trifurcatum illustrating the distinctive trifurrowed bioglyph patterns (mainly comprising lateral stroke marks LSL and LSR) that characterize this dwelling-burrow and manifest its excavation (cf. Plates 17 & 18). The lateral stroke patterns were produced by three long fingers or toes (digits II, III, and IV) from both forelimbs (left and right) of an amphibian or amphibian-like reptile. Frontal strokes (FS) and beak scrapes (BS) are not evident.


LSR
LSL
FS
CRL
CFRL
BREADTH
NO WALL-LAYER
LENGTH
DORSAL
LEFT SIDE
INTERPRETATION
0
3 cm
ENLARGEMENT
DORSAL VIEW
RIGHT SIDE
VENTRAL
0·8 cm
WIDTH
LEFT SIDE
0
3 cm
DORSAL
BASAL VIEW

TEXT-FIG. 6.8.



TEXT-FIG. 6.9. Oblique apertural view (from the dorsal side) of the large dwelling-burrow <u>Pytiniichnus trifurcatum</u> and reconstruction of its inferred reptile-like amphibian producer shown together with the bioglyph patterns it produced during burrow excavation. The size of the animal, as depicted, is not necessarily accurate relative to the size of the burrow. Drawing is based on the holotype burrow in the composite burrow specimen shown in Plate 18 Fig. b.


LSR
LSL
FS, CRL & CFRL
NO WALL LAYER
PASSIVELY INFILLED RED CLAY
VENTRAL
WIDTH.
BREADTH.
RIGHT SIDE.
LEFT SIDE.
0 1 2 3cm.
DORSAL.
OBLIQUE VIEW.

TEXT-FIG. 6.9.

burrows the dimensions are quite similar: the incomplete lengths and 7 cm and 8 cm respectively, the fully-preserved breadths are 14 cm and 15 cm, and the fully-preserved widths and 5 cm and 5.5 cm (Table 6.4). No wall-layer is present, in contrast to both species of Turimettichnus. The organism occupied the whole cavity of the excavation (i.e., the dwelling ratio is effectively 100%; Table 6.4). No enlargement such as might constitute a turn-around is present. Entry to and exit from the burrow occurred with the animal's body in the same head-downward orientation (Text-Figs.1.9 & 6.10). The base of the burrow is somewhat U-shaped or rounded.

(2) The bioglyphs and their interpretation: The trifurrowed bioglyph pattern is conspicuous on the outer surface of the burrow and is better preserved on the dorsal rather than the ventral surface (Plates 17 & 18). Its preservation has been brought about by subsequent infilling of the burrow with sediment. The bioglyph pattern is distinctly different from those in Turimettichnus in that the stroke marks are trifurrowed and the individual furrows are relatively wide and arcuate in transverse section (Text-Fig. 6.11). Each of the three furrows that define an individual stroke movement are parallel. The trifurrowed impression presumably resulted exclusively from digging activity as indicated by the absence of evidence of contact with the host sediment by the other two digits (i.e., digits I and V) which were probably too short to be effective (Text-Fig. 6.8).

This type of three-digit pattern can only have resulted from organisms such as burrowing amphibians or reptiles. The producing organism presumably had three long digits in the middle, flanked by two short digits on either side of a row of longer digits (cf. Text-Fig. 6.8), and thus a total of five digits on each limb. The parallel strokes of the right forelimb are imprinted on the right side of the burrow and similarly the parallel strokes of the left forelimb occur on the left side of the burrow (cf. Text-Figs. 6.8 - 6.10). Each of these stroke marks overlap on the middle part of the dorsal side and the base of the burrow to form a combination pattern (CRL; see Text-Fig. 6.2; and Plate 17 and Plate 18 Fig.a). These left and right stroke patterns are imprinted on the respective sides of the burrow resulting from the digging activity of both forelimbs along the length of the burrow during all stages of its excavation (cf. Text-Fig. 6.10B).

<u>(3) Absence of a wall-lining and palaeoecological implications:</u> <u>Pytiniichnus trifurcatum</u> has no wall-lining and hence the burrow has no protection from the surrounding conditions. The absence of a thick reinforcing wall-layer in this ichnogenus is probably explained by the following considerations: (1) the burrow was excavated in a subaerial location in clayey soil and hence was not as prone to gravitational collapse as it would have been in subaqueous conditions; (2) thigmotaxis effects were less significant in this subaerial environment as indicated by the absence of associated burrows. Wall-linings are known to be established in some vertebrate burrows, especially those produced by lung-fish (Smith , 1931; Johnels & Svensson, 1955; Vohies, 1975; and Dubiel et al., 1987) but, with the exception of the therapsid burrows described by Smith (1987), they lack bioglyphs.

TEXT-FIG. 6.10. Reconstructed excavation mechanics and producer animal's entry and exit from the burrow Pytiniichnus trifurcatum.

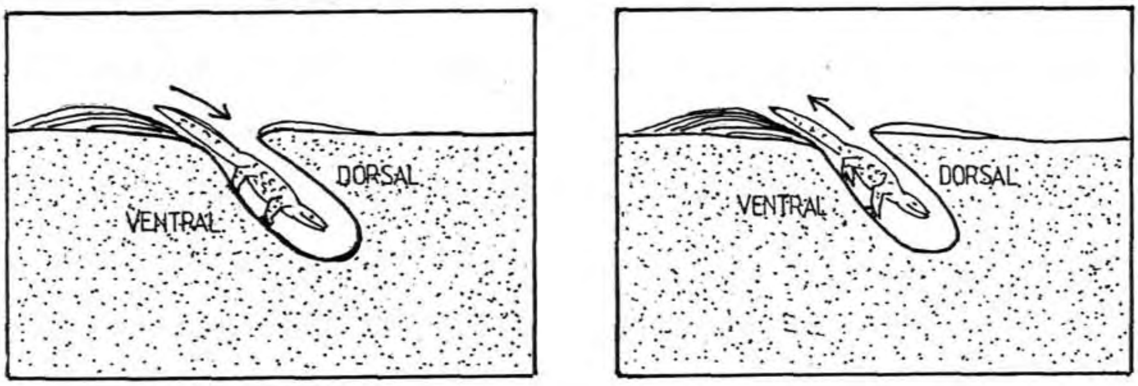
A. Reconstructed orientation of the inferred reptile-like amphibian producer during entry to and exit from the burrow (no necessity for a turn-around). Because the burrow lacks a bulbous termination that might have functioned as a turn-around it is inferred that the animal's entry to and exit from the burrow was in a common, probably head-downwards, orientation.

B. Reconstructed formation of the trifurrowed bioglyphs produced by stroke movements of the left and right forelimbs of the organism during excavation.

A ORIENTATION OF ORGANISM DURING ENTRY AND EXIT

ENTRY TO BURROW

EXIT FROM BURROW



ENTRY MOVEMENT
(HEAD DOWNWARD)
FORWARD ORIENTED POSITION

EXIT MOVEMENT
(TAIL UPWARD)
BACKWARD ORIENTED POSITION

SIDE VIEW

← MOVEMENT DIRECTION OF ORGANISM

B

RIGHT-MANUS SIDE STROKES

LEFT-MANUS SIDE STROKES

TOP VIEW

TEXT-FIG. 6.10.

MOVEMENT DIRECTION OF ORGANISM
MOVEMENT OF FORELIMBS DURING EXCAVATION; LARGER ARROWS INDICATE DIGGING STROKE.

Comparison: No other known burrow produced by vertebrates (including the burrows of amphibians and amphibian-like reptiles; cf. Voorhies, 1975; and Chamberlain, 1975) is strictly comparable with the form described here. The small dicynodont helicoidal burrow of therapsid (mammalian-like reptile) origin (Smith, 1987) from the Late Permian of South Africa is the only near-comparable ichnogenus known to date. Whether Pytiniichnus trifurcatum was also excavated by some other type of dicynodont animal is a question without answer since, unlike the burrows described by Smith, the composite burrows of Pytiniichnus described here show no evidence of body fossil remains. The new ichnogenus is established on three ichnotaxonomic grounds: firstly, the intrinsically different pattern of bioglyphs (trifurrowed rather than monofurrowed); secondly, the non-helicoidal configuration of the burrow in contrast to the burrows described by Smith (1987); and thirdly, the absence of a thick wall-lining (in contrast to Turimettichnus), the burrow having been established in a subaerial situation above the grond-water-table and simply infilled by red clay from the associated palaeosol (see below).

Material studied: Only one specimen containing two intersecting burrows has been discovered and this was located within palaeosol horizons in the upper part of the Bald Hill Claystone at Long Reef Point (area 3). This comprises the holotype specimen (burrow 1) and paratype specimen (burrow 2), 303/MU.44365.

Distribution: P. trifurcatum is presently known only from palaeosol horizons of trace fossil subinterval IC5? of the Bald Hill Claystone at Long Reef.

Preservation and association: P. trifurcatum is preserved as a full-relief form in palaeosol sediment exposed on the southern cliffline at Long Reef. It is not association there with Turimettichnus or any other trace fossils.

Ichnofacies and palaeoenvironmental affinities: P. trifurcatum belongs to the Scoyenia ichnofacies (Seilacher, 1967) which trace fossil association was originally stipulated to characterize continental redbeds and similar deposits. Subsequently, through indiscriminate usage, the concept of the ichnofacies Scoyenia was gradually broadened to embrace all nonmarine assemblages in general. The current interpretation of most workers is that trace makers of the Scoyenia ichnofacies manifest exploitation of moist to wet areas such as low-lying subaerial deposits subject to inundation by flood waters or shallowly submerged substrates subject to periodic subaerial exposure. The single composite burrow of P. trifurcatum so far discovered in the study area occurred within the upper part of the Bald Hill Claystone at Long Reef described and interpreted by Retallack (1976 & 1977) as comprising a sustained interval of palaeosols. The inferred amphibian or amphibian-like reptile origin of the Pytiniichnus burrows and the absence of burrows of any other kind in the enclosing redbed strata are consistent with Retallack's palaeosol interpretation of this upper part of the Bald Hill Claystone at Long Reef and hence the subaerial as opposed to subaqueous setting of the substrate in which the burrows were excavated.

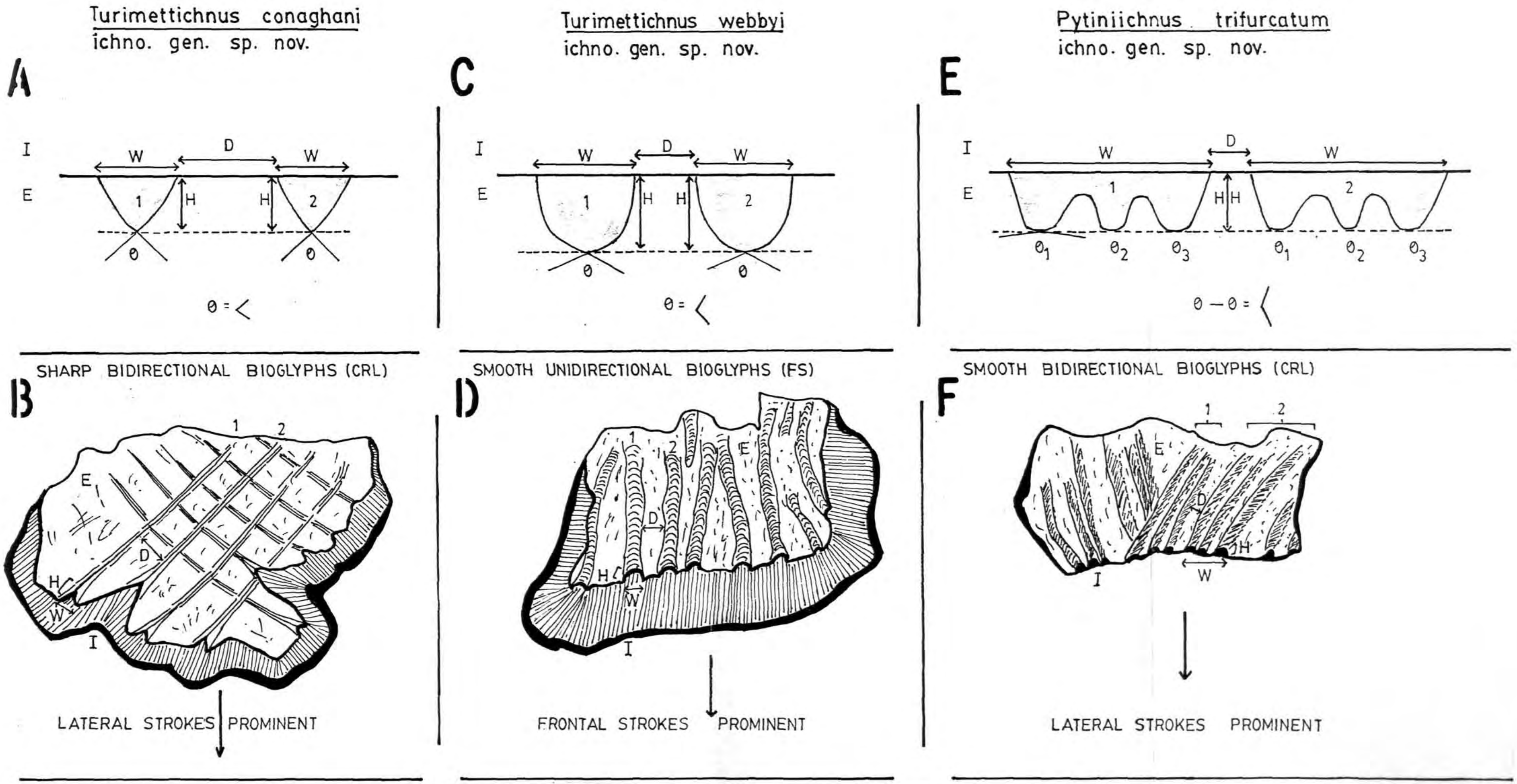
TABLE 6.4. Table documenting the dimensions of the two new ichnogenera <u>Turimettichnus</u> and <u>Pytiniichnus</u>. A comparative volumetric study shows that <u>T. webbyi</u> has more volume for dwelling than does <u>T. conaghani</u>. The other new ichnogenus, <u>Pytiniichnus</u>, potentially utilises the whole of the excavation for accupation since (in contrast to <u>Turimettichnus</u>) none of its volume is taken up by a wall-lining. Details of the arithmetic calculations involved in deriving the various dimensional parameters are indicated by short equations (involving column numbers 1 to 9) at the top of each relevant column.

No.	Ichnogenera <u>T. conaghani</u> <u>T. webbyi</u> <u>P. trifurcatum</u>	MU. no. Sample no.	MEASUREMENT										Intv. Sub-intv.	Locality.
			BURROW EXCAVATION				LIVING CHAMBER							
			1	2	3	4	5	6	7	8	9	10		
			L (cm)	B (cm)	W (cm)	Total vol/ area. (1x2x3) (cm3)	L (cm)	B (cm)	W (cm)	Total vol/ area. (5x6x7) (cm3)	Wall layer (cm)	Dwelling ratio (%) (8÷4)		
1.	<u>T. conaghani</u> var.A	MU.44351 Sp.212	26	13	8	2704	24.6	10.2	5.2	1304	1.4	48	C3 & C4	Turimetta Head
2.	<u>T. conaghani</u> var.B	MU.44352 Sp.213	47	18	8	6768	45.8	16.8	6.8	5232	1.2	77	"	"
3.	<u>T. conaghani</u> var.A	MU.44355 Sp.209b	11	11	5	605	9.4	9.4	3.4	300	1.6	50	C2	"
4.	<u>T. conaghani</u> var.B	MU.44353 Sp.215	28	12	6.3	2117	26.0	10.0	4.3	1118	2.0	53	C2	"
5.	<u>T. conaghani</u> var.B	MU.44354 Sp.216	8.5	12	5	510	7.1	10.6	3.6	270	2(D) 0.8(V) 1.4(avg)	53	C4	"
1.	<u>T. webbyi</u>	MU.44356 Sp.209a	17.0	26	14	6188	1.5	23.5	11.5	3918	2.5	64	C2	"
1.	<u>T. conaghani?</u>	MU.44357 Sp.211	x	16.7	7.8	130	x	15.5	6.3	97	1.5	75	C4	"
2.	<u>T. conaghani?</u>	From exposure.	x	25.0	15.0	375	x	22.5	12.5	281	2.5	75	C2	"
3.	<u>T. conaghani?</u>	"	x	20.0	14.0	280	x	17.5	11.5	201	2.5	72	C2	"
1.	<u>P. trifurcatum</u> (incomplete burrows)	Br.1 & Br.2 MU.44365 Sp.303	7 8	14.0 15.0	5.0 5.0	490 660	x x	x x	x x	490 660	x x	100 100	C? "	Long Reef Point

abbreviations.

L = length; B = breath; and W = width; Intv. = interval; subintv. = subinterval; and x = measurement not available.

TEXT-FIG. 6.11. Comparative morphology of the bioglyphs of the two new ichnogenera Turimettichnus and Pytiniichnus. Figs. A, C, and E are enlarged cross-sectional views showing the shape of individual furrows, and Figs. B, D, and F are oblique views of the different bioglyph patterns as preserved in bass-relief through active wall-lining burial in mud (B and D) and passive sediment infilling of the burrow (F). Views are from the outside of the burrow looking obliquely inwards toward the burrow interior.



D	Distance between two bioglyph furrows.
H	Furrow relief.
W	Furrow width.
I	Interior side of the burrow.
E	Exterior sides of the burrow.
θ	Apical angle of furrow.
1, 2	Bioglyph furrows made by a single stroke of the animal's appendages/fore limb: in B and D each stroke resulted in a single furrow; in F each stroke resulted in three furrows.

burrow wall-layer

passively infilled sediment

Longitudinal axis of burrow; arrow points towards base.

(Illustrations are not in scale).

TEXT-FIG. 6.11