CHAPTER 14

ESCAPE-STRUCTURES

ESCAPE-STRUCTURES

14.1. INTRODUCTION

Structures that are characterized by downward-directed laminae and which superficially resembled animal escape-structures were just described from ancient rocks by Boyd (1966, p.45-46) from the Middle Cambrian Flat Head Sandstone of Wyoming USA. By way of attempting to explain these structures Boyd (ibid) performed experiments which indicated that the downwarping and truncation of laminae in the Flat Head Sandstone burrows probably resulted from the subsurface removal of sediment, although the mechanism for this inferred removal in the case of the Flat Head Sandstone burrows could not be satisfactorily explained. Hallam and Swett (1966, p.103-106) described similar structures regarded by them as trace fossils from the Lower Cambrian Pipe Rock of Scotland, which they assigned to the genus Monocraterion. Structures of this type were regarded by Hanor & Marshall (1971, p. 128, fig. 16) as structure formed by shearing.

Schäfer (1972, p. 288, fig.165) noted that the modern cerianthid anemone Cerianthus deflects sediment downwards and truncates laminae during both upward and downward burrowing activity for escape purposes. Shinn (1968) studied the escape-burrows of another actinian sea anemone, Phyllactis conguilagia, living on the Bahama banks. Curran & Frey (1975), described very large `escape-structure' from the Pleistocene of North Carolina which differed from those mentioned above by virtue of the presence of numerous downward-deflected laminae that could be traced continuously across longitudinal sections of the structure, i.e., the laminae were not truncated across the axis of the burrow. This type of configuration of downward-deflected continuous laminae can form inorganically through collapse of sediment overlying a burrow upon or subsequent to the burrow being vacated by its animal inhabitant and are called `collapse-structures' (see Text-Fig. 14.7, Plate 44 Fig. b, and Plate 78 Fig. c). This latter type of inorganic collapse-structure can be strikingly similar in geometry to the structures produced by the collapse of sediment into the open burrows of Callianassa major (Howard, 1971) which can attain very large size. But the two different kinds can be differentiated by the geometrical attitude of the laminae and the sediment texture in the central (axial) part of the structure (Kamola, 1984). The inclination of the laminae in inorganic collapse-structures decreases upwards, but in the animal escape-structures the inclination of the laminae usually remains unchanged upwards. Whereas escape burrows are commonly cast/infilled by overlying sediment and collapse-structures are commonly infilled both by overlying and laterally adjacent sediment, the geometry of the resulting V- or U-shaped layering in both can be very similar in vertical cross-section. In the case of the new ichnogenus Hannibalichnus (type B, bilobed-shaped escape-structure; Text-Fig. 14.1), an underlying bilobed escape-structure is overlain by a collapse-structure but the latter should be regarded as of only incidental importance or significance ichnotaxonomically (see Text-Fig. 9.7, and Plate 44 Fig. b).

Another problem has to do with the differentiation of vertical escape burrows characterized throughout by V- or U-shaped layering and similar vertical burrows which are characterized by only sporadic V- or U-shaped layering throughout their length and hence suggesting that such burrows manifest mainly dwelling activity punctuated by minor upward and/or downward escape activity as a consequence of the animal's need to maintain an optimum depth of burial below the sediment-water interface (cf. Text-Fig. 14.5).

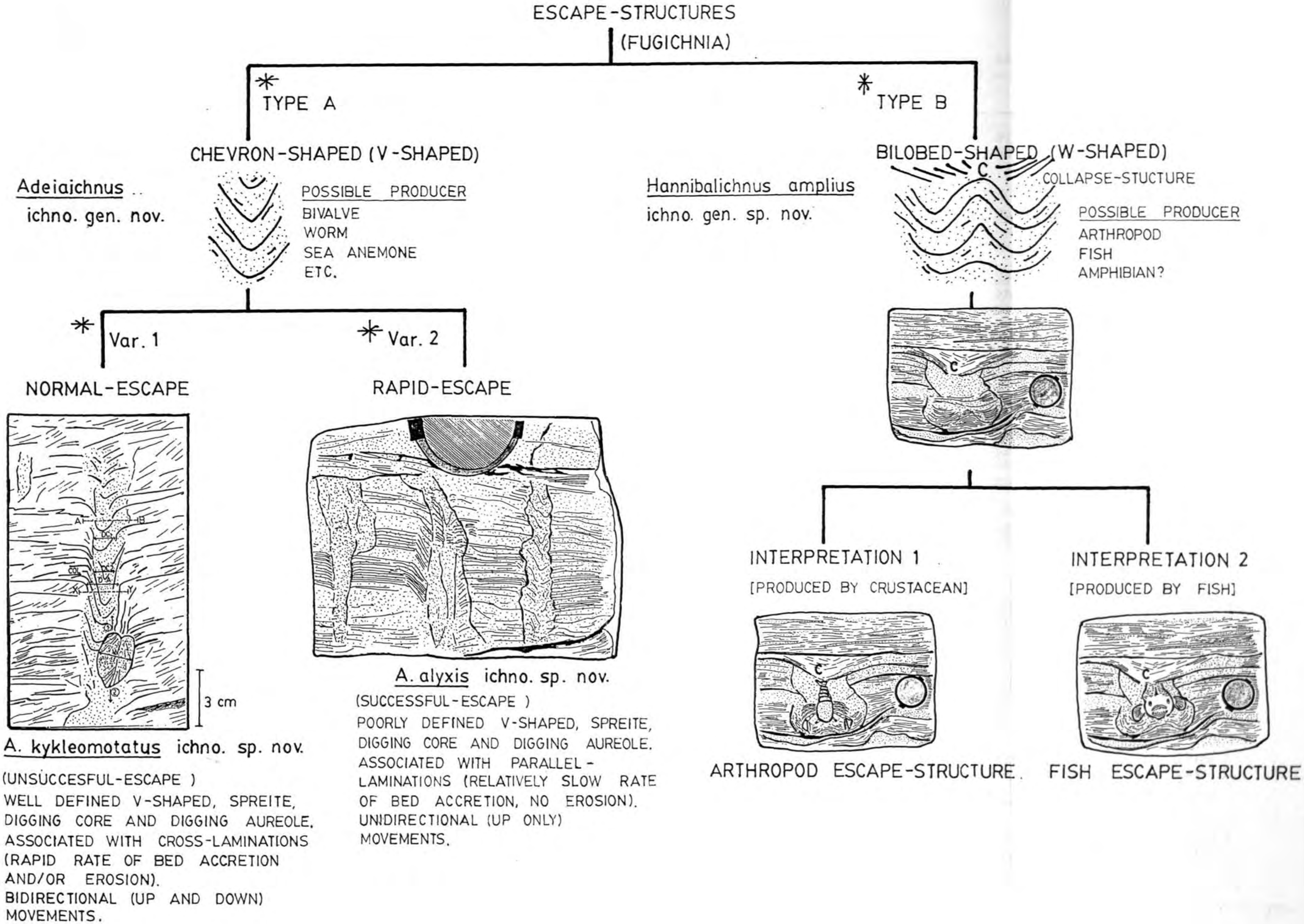
14.2. CLASSIFICATION

Based on the specimens studied here, the escape-structures can be grouped into two major categories (Text-Fig. 14.1). The first category accommodates somewhat cylindrical-shaped burrows with an internal V-shaped layering. The second category accommodates bilaterally symmetrical bilobed escape-burrows typically with depressed lateral regions separated by a raised medial ridge longitudinally along the burrow.

The first group of escape-structures which includes a new ichnogenus (Adeiaichnus) is characterized by a chevron pattern of downward-deflected laminae that probably can be produced by several different kinds of organisms such as bivalve molluscs, worms, sea anemones (i.e., the latter including elongated worm-like forms such as Cerianthus Fürsich, 1972, p.289, fig. 165). This category can be further divided into two subgroups on thebasis of different ethological criteria. The first subgroup contains the new ichnospecies A. Kykleomotatus, which is defined by its well defined V-shaped laminations and other internal structures (i.e., digging core and digging aureole). These internal structures are normally well developed because of the nature

TEXT-FIG. 14.1. Proposed classification of escape-structures characterized by V-shaped internal layering, termed here respectively Type A and type B. The classification is mainly based on the morphology of the burrow which grossly reflects the size and morphology of the producer organism. Type A escape-structures belong to the new ichnogenus Adeiaichnus which can be subdivided into two ichnospecies on the basic ethological criteria. The first new ichnospecies A. Kykleomotatus, manifests repeated upward and downward motion and the second new ichnospecies, A. alyxis manifests rapid successful escape. Type B escape-structures belong to the new bilobed ichnogenus Hannibalichnus amplius. The producer organism the type B escape-structure can be variously as an arthropod (crustacean) or a fish or possibly even an amphibian. Collapse-structures (C) occurs immediately above the Type B escape-burrow. except for animal reconstructions in diagrams at bottom-right, details of all sketches are based on photographs of field exposures. Lens cap diameter = 5 cm) gives scale in all diagrams except that at left.

The various features and criteria used at the different ichnotaxonomic levels in the classification and the rationale and justification for their selection are elaborated in Table 14.1.


ESCAPE-STRUCTURES
(FUGICHNIA)
TYPE A
TYPE B
CHEVRON-SHAPED (V-SHAPED)
Adeiaichnus ichno. gen. nov.
POSSIBLE PRODUCER
BIVALVE
WORM
SEA ANEMONE
ETC.
BILOBED-SHAPED (W-SHAPED)
COLLAPSE-STUCTURE
Hannibalichnus amplius ichno. gen. sp. nov.
POSSIBLE PRODUCER
ARTHROPOD
FISH
AMPHIBIAN?
Var. 1
Var. 2
NORMAL-ESCAPE
RAPID-ESCAPE
3 cm
A. kykleomotatus ichno. sp. nov.
(UNSUCCESFUL-ESCAPE)
WELL DEFINED V-SHAPED, SPREITE, DIGGING CORE AND DIGGING AUREOLE. ASSOCIATED WITH CROSS-LAMINATIONS (RAPID RATE OF BED ACCRETION AND/OR EROSION). BIDIRECTIONAL (UP AND DOWN) MOVEMENTS.
A. alyxis ichno. sp. nov.
(SUCCESSFUL-ESCAPE)
POORLY DEFINED V-SHAPED, SPREITE, DIGGING CORE AND DIGGING AUREOLE. ASSOCIATED WITH PARALLEL-LAMINATIONS (RELATIVELY SLOW RATE OF BED ACCRETION, NO EROSION). UNIDIRECTIONAL (UP ONLY) MOVEMENTS.
INTERPRETATION 1
[PRODUCED BY CRUSTACEAN]
INTERPRETATION 2
[PRODUCED BY FISH]
ARTHROPOD ESCAPE-STRUCTURE.
FISH ESCAPE-STRUCTURE.

TEXT - FIG. 14.1.

of the movements of the organism. The organism is periodically forced to move either upward or downward as a consequence respectively of sedimentation and erosion. In this way it maintains a constant position relative to the sediment-water interface during rapidly shoaling or eroding conditions (i.e., involving especially bedload sediment movement) and thus escapes burial or exposure. Study of the ripple cross-laminated specimen illustrated in Text-Fig. 14.5 and Plates 40 and 41 suggests that bedload accretion of the sediment was relatively rapid and simply trapped the producer bivalve mollusc inside its burrow (i.e., unsuccessful escape-structure). The second subgroup accommodates poorly defined escape-structures. This type of structure is formed by an organism which is forced consistently by sediment accretion to move progressively upward in order to maintain a constant position relative to the sediment-water interface and hence escape burial. This type of structure is associated with parallel-laminated substrates that reflect sediment accretion mainly through slow to moderate accumulation rates of suspended-load sediment thus guaranteeing the animal's ability ultimately to escape from the burrow and find a new burrow site (i.e., successful escape-structure).

Previously there has been no systematic scientific classification of these escape-burrows, but in the proposed classification scheme they are accorded an important ethological status (Text-Fig. 14.1). The newly described type specimens on which the proposed classification is based are well preserved in cross-laminated and parallel-laminated siltstone and very fine

TABLE. 14.1. Rationale approach and various features used at the ichnotaxonomic levels in the proposed classification of escape-structures (fugichnia).

Escape-structure (fugichnia) Simpson, 1975 (group level above ichnogenus).

I. Significant features (generic level).

General shape of the escape-traces and their internal structures (refers to the producers).

(1) V-shaped (inverted cone-shaped) or chevron-shaped.
(2) W-shaped or bilobed-shaped.

II. Major accessory features (species level).

Definition of the internal structures.

(1) Well or poorly defined (continuous or discontinuous nature) V-shaped or W-shaped structure.
(2) Presence/absence of spreite and its defination (continuous or discontinuous).
(3) Well or poorly defined digging core and digging aureole.
(4) Well or poorly defined boundary of the burrow with the host rocks.

III. Minor accessory features (lower species level or variety level).

Relative movements of the producer organism.

(1) Unidirectional (i.e., either upwards or downwards).
(2) Bidirectional (i.e., upwards and downwards).

IV. Other features.

(1) Evidence of successful/unsuccessful escape (i.e., producer organism either absent or trap inside the burrow).
(2) Evidence of bed accretion/degradation rate at time of escape or attempted escape defined by associated sedimentary structures: e.g. cross-lamination/bedding or parallel-lamination (during accretion); scour relief (during degradation).
(3) Presence/absence of a collapse structure above the escape structure.
(4) Type of infilled sediments. Infilling sediment similar/dissimilar to host sediment.
(5) Source of infilling sediments (i.e., above or laterally adjacent).

TABLE 14.2. Tabulation of diagnostic salient characteristics of various structures inferred here and/or in the literature to be of animal-escape origin together with their previous names (where applicable) and new and/or revised names in terms of the proposed classification.

No.	Producer	Ethological classification	Internal layering (V/W-shaped)	Definition of internal structures	Previous names or assignment	Proposed scientific names	Remarks
1.	Arthropod	Fugichnia	W-shaped, small (3 cm width)	Well-defined bilobed-shaped	Chagrinichnites osgoodi Hannibal & Fieldmann, 1983.	Hannibalichnus osgoodi (Hannibal & Fieldmann, 1983)	C. brooksi (cubichnia)
2.	Arthropod (crustacean) or fish	Fugichnia	W-shaped, large (10 cm width)	Well-defined bilobed-shaped	ichno. gen. sp. nov.	Hannibalichnus amplius ichno. gen. sp. nov.	Type B
3.	Xiphosurid	Fugichnia	W-shaped, large	well-defined bilobed-shaped	Aulichnites bradfordensis (Chisholm, 1985, pl.75, text-fig.1; pl.76, text-fig.1)	"	Type B
4.	Bivalve (mollusc)	Fugichnia	V-shaped, small (1-3 cm width)	Well-defined digging core, digging aureole with well defined V-shaped laminations	ichno. gen. sp. nov.	Adeieichnus kykleomotatus ichno. gen. sp. nov.	Type A var. 1
5.	Bivalve (mollusc)	Fugichnia	V-shaped, small (1-3 cm width)	Poorly defined V-shaped layers, dig--ging core and aureole	ichno. gen. sp. nov.	Adeieichnus alyxis	Type A var. 2
6.	Bivalve (mollusc)	Fugichnia	V-shaped, small (1-3 cm width)	Well-defined V-shaped layers, digging core and aureole	Pelecypodichnus Seilacher, 1953, and Eager, 1974	Adeieichnus kykleomotatus ichno. gen. sp. nov.	Type A var. 1
7.	Bivalve (mollusc)	Fugichnia	V-shaped, small (1-3 cm width)	Poorly defined V-shaped layers, digging core and aureole	Pelecypodichnus Seilacher, 1953, and Eager et al., 1985	Adeieichnus alyxis ichno. gen. sp. nov.	Type A var. 2
8.	Bivalve (mollusc)	Fugichnia	V-shaped, small (1-3 cm width)	Well defined V-shaped laminations	'Bivalve trace fossils' Thoms & Bergs, 1985	Adeieichnus kykleomotatus ichno. gen. sp. nov.	Type A var. 1
9.	Bivalve (mollusc)	Fugichnia	V- or U-shaped, small (1-3 cm width)	Well-defined V-shaped laminations	'Escape trace' Carey, 1978	Adeieichnus kykleomotatus	Type A var. 1

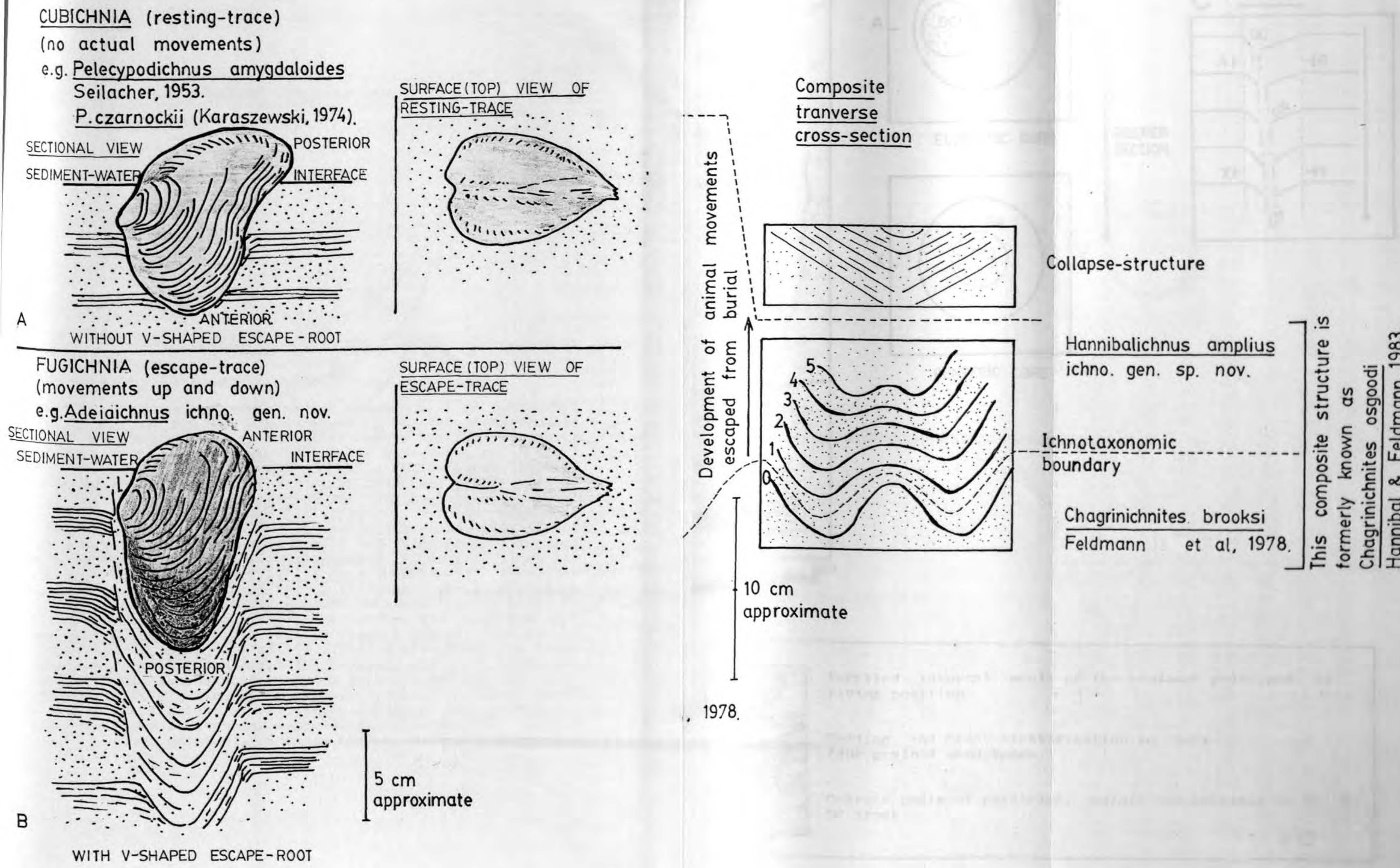
TABLE 14.2 (continued)

No.	Producer	Ethological classification	Internal layering (V/W-shaped)	Definition of internal structures	Previous names or assignment	Proposed scientific names	Remarks
10.	Bivalve (mollusc)	Fugichnia	V-shaped; small (1-3 cm width)	Poorly defined digging core, aureole and V-shaped laminations	`Escape structures' McCarthy, 1979	<u>Adeieichnus alyxis</u> ichno. gen. sp. nov.	Type A var. 1
11.	?	?	V-shaped, very large width	Well defined V-shaped laminations with no disruption of the 'V'	`Escape burrow' Curran & Frey, 1975	Inorganic (non-biogenic sedimentary structures	Type ?

TEXT-FIG. 14.2. Schematic illustration of the similarity bivalve mollusc resting-structure and its escape-structure as viewed in horizontal transverse cross-sections. AS originally defined the ichnogenus *Pelecypodichnus amygdaloides* (Seilacher, 1953) refers only to the cubichnia (resting-trace) category of the bivalve (cf. in Fig. A). This type of heart-shaped structure is in some cases associated with a nested series of V-shaped escape-traces (cf. Fig. B). The underlying V-shaped escape-traces thus belong to a different ethological category (fugichnia or escape-structure, Simpson, 1975) than does the associated resting traces and must therefore be given different ichnotaxonomical name to that of the resting trace. The illustration explains the importance and necessity of establishing a new ichnogenus (*Adeiaichnus*) for the escape-structure in the present classification.

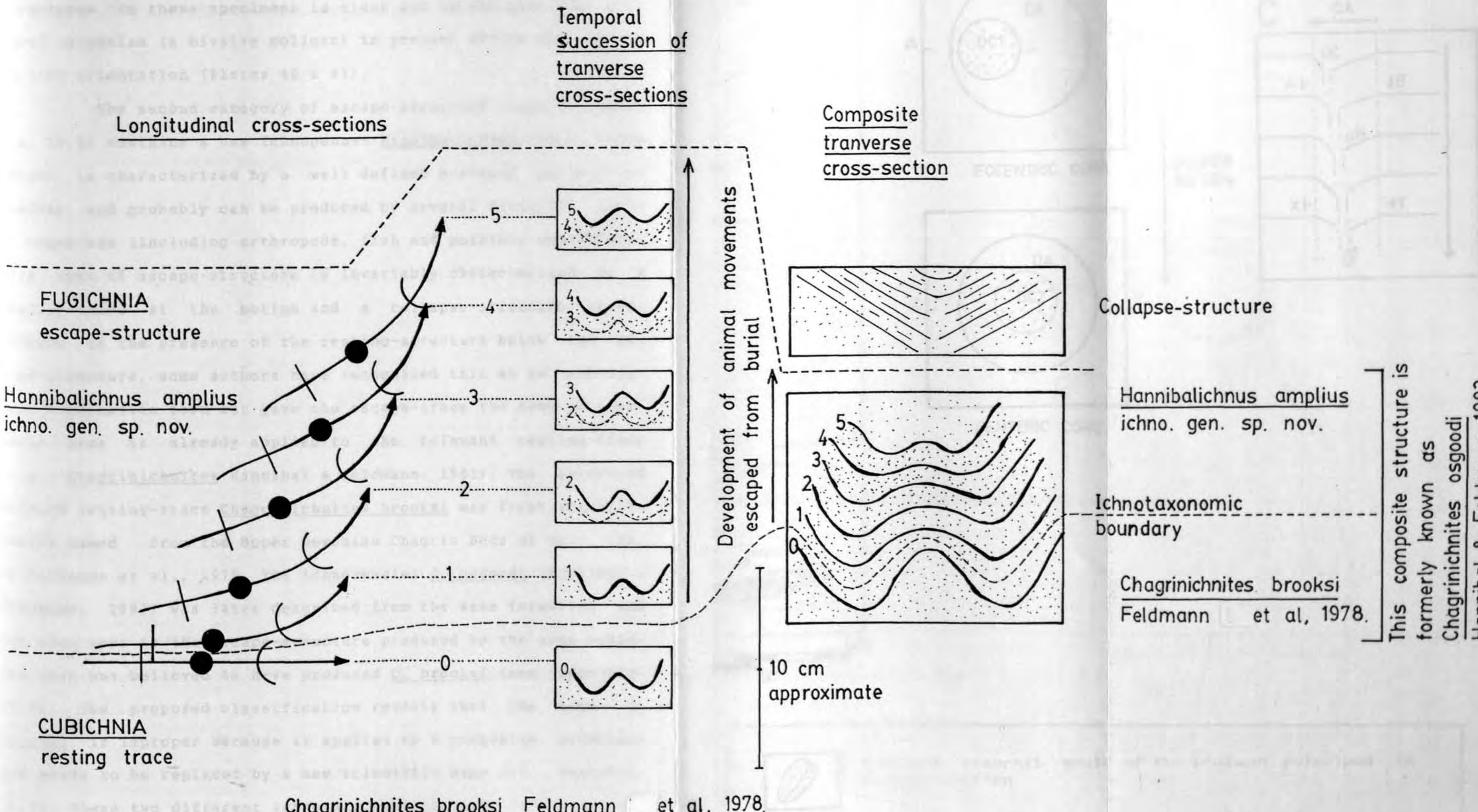
Escape potentials range from less than 5 cm depth in most epifaunal suspension-feeders to more than 50 cm depth in some infaunal siphonate-feeders. The major factors controlling the escape potential are: (1) type of bivalve feeding group; (2) degree of mantle fusion; (3) siphon formation; and (4) types of sediment. Size of the bivalve mollusc and water temperature are generally of lesser importance (Kranz, 1970).

Examination of the sedimentary structures formed by bivalves (Thoms & Berg, 1985) reveals that in vertical section (Fig. B, left side). They compare a nested series of inverted cones. In bedding-plane (Fig. B, right side) the structure has the appearance of a cross-sectional outline of a bivalve shell (heart-shaped).


CUBICHNIA (resting-trace)
(no actual movements)
e.g. Pelecypodichnus amygdaloides
Seilacher, 1953.
P. czarnockii (Karaszewski, 1974).
SECTIONAL VIEW
POSTERIOR
SEDIMENT-WATER INTERFACE
ANTERIOR
A
WITHOUT V-SHAPED ESCAPE-ROOT
SURFACE (TOP) VIEW OF RESTING-TRACE
FUGICHNIA (escape-trace)
(movements up and down)
e.g. Adeiaichnus ichno. gen. nov.
SECTIONAL VIEW
ANTERIOR
SEDIMENT-WATER INTERFACE
POSTERIOR
SURFACE (TOP) VIEW OF ESCAPE-TRACE
5 cm approximate
B
WITH V-SHAPED ESCAPE-ROOT
Composite tranverse cross-section
Development of animal movements escaped from burial
Collapse-structure
5
4
3
2
1
0
Hannibalichnus amplius ichno. gen. sp. nov.
Ichnotaxonomic boundary
Chagrinichnites brooksi Feldmann et al, 1978.
This composite structure is formerly known as Chagrinichnites osgoodi Hannibal & Feldmann, 1983.
10 cm approximate
1978.

TEXT-FIG. 14.2.

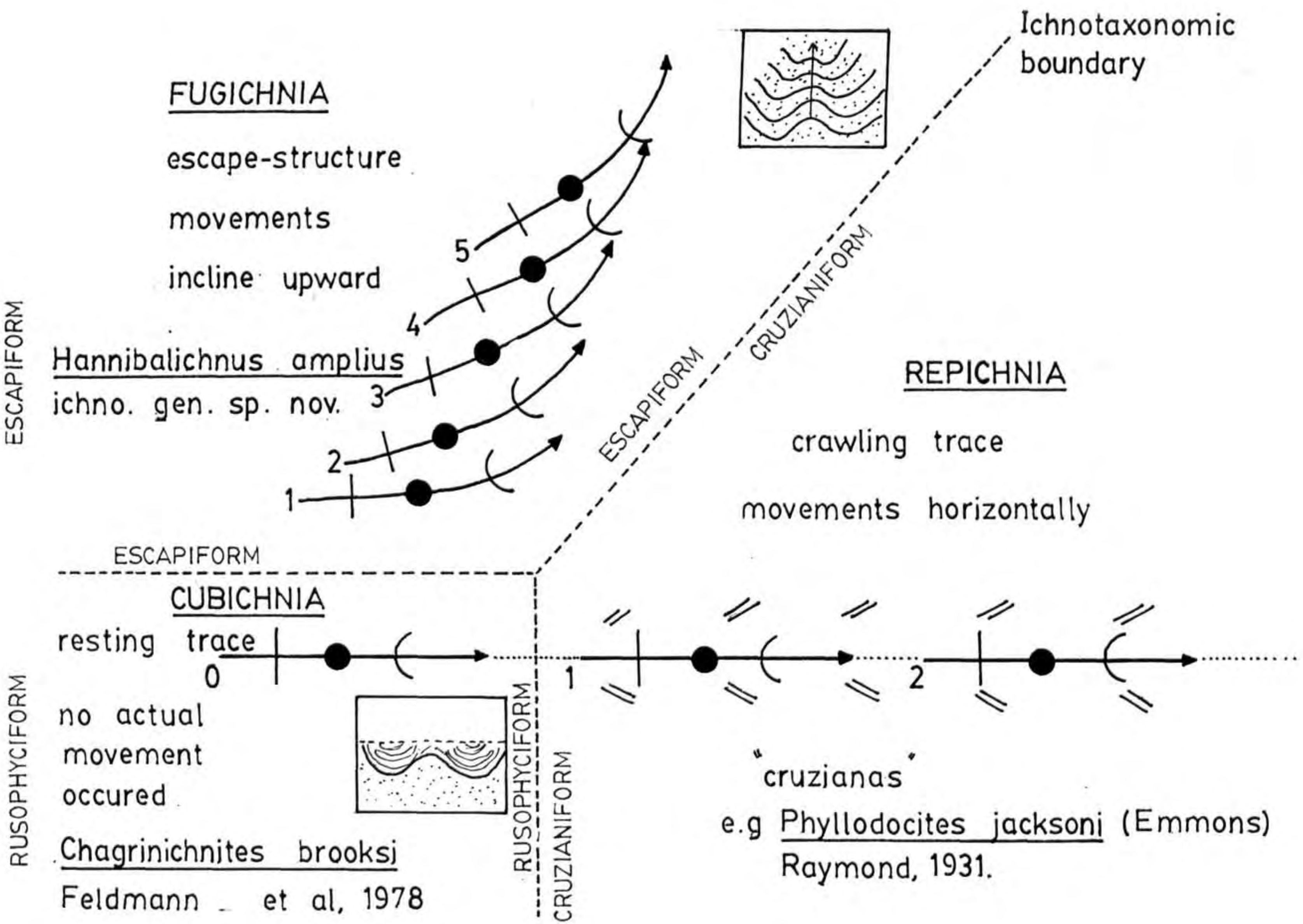
TEXT-FIG. 14.3. Schematic illustration designed to explain the transitional relationship between a resting-structure and its associated bilobed escape-structure as seen in both longitudinal (left) and transverse (right) cross-sections. The W-shaped or bilobed-shaped escape-structure Chagrinichnites brooksi Feldmann et al., (1978) was first established for arthropod resting structures. Later Hannibal and Feldmann (1983) described escape-structures of this ichnogenus and gave them the name C. osgoodi. However the latter structures do not belong to the resting-trace category (cubichnia) but belong instead to the escape-structure category (fugichnia, Simpson, 1975), and must therefore have a different ichnotaxonomical it is important and necessary to establish a new ichnogenus to accommodate the specific behavior of the producer organism. The new ichnogenus Hannibalichnus (for J.T. Hannibal, who described the first bilobed escape-structures) is erected in the present classification to differentiate the trace of the escape behavior of the arthropod or arthropod-like organisms from the trace of its resting behavior. Lower dashed line defines the inferred boundary between two the ichnogenera. These types of escape-structure are normally overlain by a collapse-structure on (shown schematically at top-right). The upper dashed line defines the inferred boundary between the escape-structure and the overlying collapse-structure.


Temporal succession of tranverse cross-sections
Longitudinal cross-sections
Composite tranverse cross-section
FUGICHNIA
escape-structure
Hannibalichnus amplius
ichno. gen. sp. nov.
CUBICHNIA
resting trace
Development of animal movements escaped from burial
Collapse-structure
Hannibalichnus amplius
ichno. gen. sp. nov.
Ichnotaxonomic boundary
Chagrinichnites brooksi
Feldmann et al, 1978.
This composite structure is formerly known as Chagrinichnites osgoodi Hannibal & Feldmann, 1983.
10 cm
approximate
Chagrinichnites brooksi Feldmann et al, 1978.

TEXT-FIG. 14.3

sandstone (Plates 40 & 41). The definition of important internal structures in these specimens is clear and in one case the producer organism (a bivalve mollusc) is present inside the burrow in life orientation (Plates 40 & 41).

The second category of escape-structure (type B; Text-Fig. 14.1) contains a new ichnogenus: Hannibalichnus. This trace fossil is characterized by a well defined W-shaped pattern of laminae, and probably can be produced by several different types of organisms (including arthropods, fish and possibly amphibian). This type of escape-structure is invariably characterized by a resting-trace at the bottom and a collapse-structure above. Because of the presence of the resting-structure below the escape-structure, some authors have recognized this as an ethological combination form but gave the escape-trace the same ichnogeneric name as already applied to the relevant resting-trace (e.g., Chagrinichnites Hannibal & Feldmann, 1983). The arthropod bilobed resting-trace Chagrinichnites brooksi was first scientifically named from the Upper Devonian Chagrin Beds of Ohio, USA, by Feldmann et al., 1978. The ichnospecies C. osgoodi (Hannibal & Feldmann, 1983) was later described from the same formation and the same area as the escape-structure produced by the same organism that was believed to have produced C. brooksi (see Text-Fig. 14.3). The proposed classification reveals that the name C. osgoodi is improper because it applies to a composite structure and needs to be replaced by a new scientific name (cf. Text-Fig. 14.3). These two different ichnotaxa from the same formation and same area must have two different ichnogeneric names: the name C. brooksi (Feldmann et al., 1978) refers to a cubichnia (i.e., TEXT-FIG. 14.4. Schematic illustration designed to explain the transitional between an escape-structure (fugichnia; top-left), a resting-structure (cubichnia; bottom-left), and a crawling-trace (repichnia; bottom-right). The inferred ichnotaxonomic boundaries between these transitional behavioral structures are defined by the dashed-lines. The structures depicted in the small boxes are transverse cross-sectional views of the different relative ichnogenera. The new ichnogenus Hannibalichnus amplius (which is comparatively larger than the type species , i.e., Hannibalichnus osgoodi -- see Table 14.2)) is a type B escape-structure in the present classification detailed in Text-Fig.14.1.


Ichnotaxonomic
boundary
FUGICHNIA
escape-structure
movements
incline upward
Hannibalichnus amplius
ichno. gen. sp. nov.
1
2
3
4
5
ESCAPIFORM
CRUZIANIFORM
ESCAPIFORM
REPICHNIA
crawling trace
movements horizontally
ESCAPIFORM
CUBICHNIA
resting trace
0
1
2
no actual
movement
occured
RUSOPHYCIFORM
RUSOPHYCIFORM
CRUZIANIFORM
Chagrinichnites brooksi
Feldmann et al, 1978
"cruzianas"
e.g Phyllodocites jacksoni (Emmons)
Raymond, 1931.

TEXT-FIG. 14.4.

resting-trace) structure and the name C. osgoodi refers to a composite (i.e., cubichnia and fugichnia) structure (see Text-Fig. 14.3). These two trace fossils manifest two different sets of ethological behavior (i.e., resting and escape) and a proposed ichnotaxonomic boundary can be drawn to differentiate these two modes of behavior (cf. Text-Figs. 14.3 & 14.4). Similarly, the transitional boundary between resting and crawling can be differentiated (see Text-Fig. 14.6).

Similarly, an obvious transition between resting and escape activity characterizes the burrow of bivalve molluscs (cf. Text-Fig. 14.2). Normally, most bivalve mollusc resting-structures (Pelecypodichnus Seilacher, 1953 or Lockeia James, 1879) immediately underlie escape-traces. Laboratory experiments with 20 modern species of bivalves show that they burrow specifically and the burrow length ranges from 5 cm in most epifaunal suspension-feeders to more than 50 cm in some siphonate infaunal suspension feeders (Kranz, 1970). Previously these bivalve escape-structures were classified as Pelecypodichnus or Lockeia but these names were originally proposed for only the resting traces of bivalves (Eager, 1974; and Eager et al., 1985) (see also Table 14.2). A similar situation is observed in the vertically repetitive star-shaped escape-structure Asteriacites Seilacher (1953). Transitions from resting-traces to feeding-traces are also evident in the ichnogenus Diplocraterion and in the suspension-feeding variety of Rhizocorallium (i.e., Rhizocorallium jenensis var. retrosus, discussed in Chapter 7) but at the same time it can also be argued that these burrows are, in general, typical escape-structures (see Text-Figs. 7.2 & 7.3). That is, it can be argued that the genetically more appropriate ethological affinity of these burrows is with the fugichnia category rather than either domichnia or fodinichnia.

The proposed classification illustrated in Text-Fig. 14.1 is based on vertical escape-structures with V- or U-shaped internal layering (type A) and a vertical escape-structure with W-shaped internal layering (type B). The classification is focused mainly on those general morphological characteristic of the burrows which reflect the morphology of the producer organism. Type A escape-structures belong to the new ichnogenus Adeiaichnus characterized by well defined downward-deflected V-shaped laminations. This new ichnogenus can be subdivided into two ichnospecies on the basis of ethological criteria. The first new ichnospecies (A. Kykleomotatus) applies to forms showing evidence of repeated upward and downward motion and unsuccessful escape; and the second new ichnospecies (A. alyxis) applies to forms showing evidence of only upward movement and successful escape. Type B escape-structures belong to the vertical W-shaped (bilobed) new ichnogenus Hannibalichnus amplius. The bilobed shape of the Type B escape-structures admits several different possible producing organisms. (Text.Fig. 14.7): either an arthropod (crustacean) or a fish or possibly even an amphibian.

The various features used at the different ichnotaxonomic levels in the classification and the rationale and justification for their selection are elaborated in Table 14.1.

14.3. SYSTEMATIC ICHNOTAXONOMY

Adeiaichnus ichno. gen. nov.

Derivation of name: `Adeia' (Greek) meaning freedom from fear, and `ichnus' also from Greek `iknos' meaning `trace'.

Diagnosis (generic assignment): Narrow vertical shaft with nested, inverted cone- or V-shaped laminations defining an escape-trace, produced by a bivalve mollusc in moving upwards and/or downwards periodically in order to escape burial and also to maintain a constant position relative to the sediment-water interface.

Remarks (diagnostic features): Narrow vertical shaft with nested series of V-shaped laminated escape-structures, either well or poorly defined. A digging core and aureole are usually present but their definition is variable from one burrow to another; in some instances their definition can be so poor that they cannot be differentiated (Text-Figs. 14.1 & 14.6). Typically occurs in fine to very fine sandy and silty substrates which exhibit ripple cross-lamination and/or parallel-lamination (Text-Fig. 14.5). IN regard to the present study material most burrows lack preserved remains of the producer organism due presumably to the organisms' successful escape; however, one burrow contained a fossil bivalve mollusc in life orientation suggesting its unsuccessful escape.

Type species A. kykleomotatus (type A var. 1) ichno. sp. nov.

Plate 40 (topotype)
Plate 41, Figs. a - b (topotype)
Plate 42, Figs. a - b (paratypes)
Plate 70, Figs. b - c

Derivation of name: `Kykleo' (Greek) meaning repeat and `motatus' (Latin) meaning `keep moving'.

Diagnosis (specific assignment): Narrow vertical shaft containing a nested series of well defined V-shaped layer/spreite constituting an escape-structure produced by a bivalve mollusc, by moving upwards and downwards periodically in order to escape burial and to maintain a constant position relative to the sediment-water interface, especially during rapidly shoaling or degrading bottom conditions.

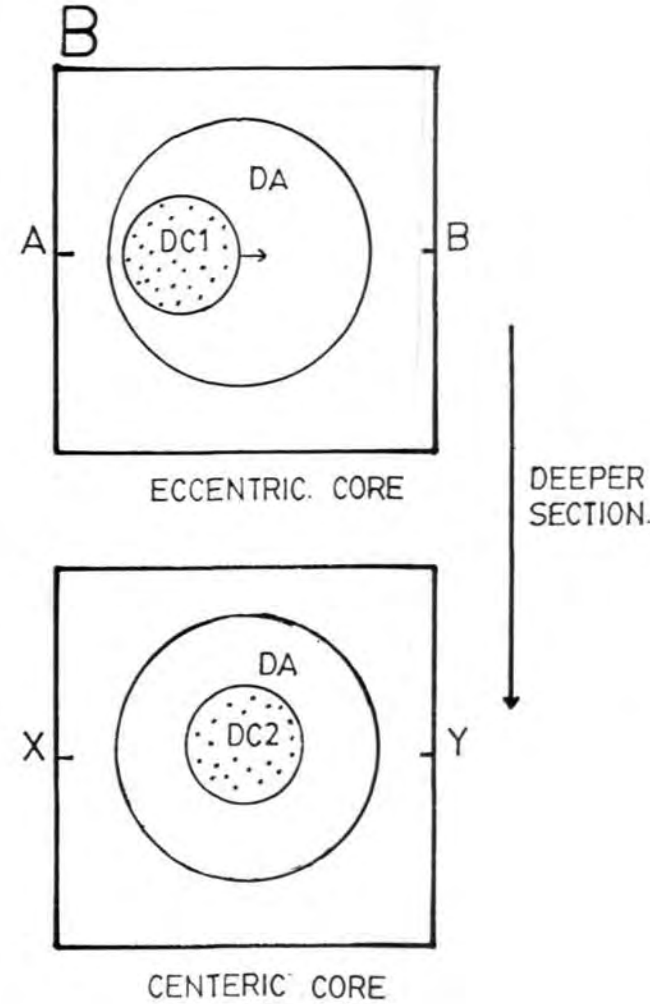
Remarks (diagnostic features): Narrow vertical shaft containing a nested series of well defined V-shaped layer/spreite and with well defined digging core and digging aureole. These structures typically occur in cross-laminated fine and very fine sand indicative of relative high rates of bed accretion and consequently the producer bivalve can be expected to have been trapped inside the burrow, as in the case of the one example from the study area (Plates 40 & 41).

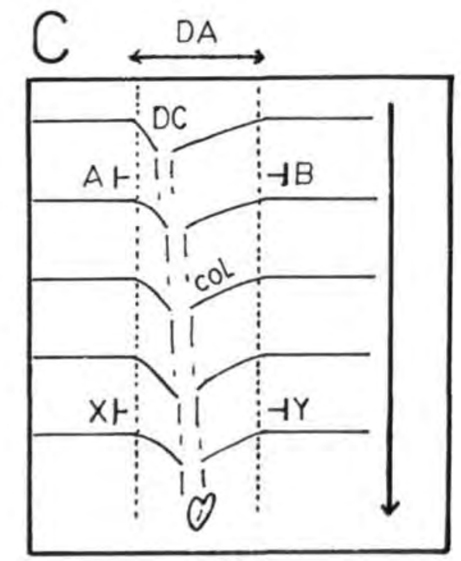
Description and ethology: This type of bivalve mollusc escape-structure is quite distinctive. In the topotype burrow (Plates 40 & 41) the width of the trace (2.5 cm) corresponds to the size of the organism (width of bivalve 2.5 cm) and the depth is about 5 cm to 15 cm from the coeval sediment-water interface. This type of escape-burrowing behavior is/was quite common in all bivalves both ancient and modern). Before making its initial burrow into the sediment the bivalve has to orientate itself into the escape-orientation which is anterior-side uppermost (this is distinctly different from the normal resting and feeding orientation which is posterior side uppermost) (Kranz, 1970). The protecting valves (shell) also help the animal to move vertically

TEXT-FIG. 14.5. **A.** Sketch made from a photograph of the type specimen of the new ichnogenus Adeiaichnus Kykleomotatus shown in Plates 40 and 41. This escape burrow belongs to the Type A, variety 1 category in the present classification (cf. Text-Fig. 14.1), i.e., the category of simple vertical burrows characterized by V-shaped internal layering and containing the fossil remains of the producer organism (because of its unsuccessful escape. The details of the structures are interpreted to mean that the organism was periodically forced to move both upward (consequent upon deposition) and downward (consequent upon erosion) in order to escape the burial and to maintain a constant position relative to the sediment-water interface during rapidly shoaling or eroding conditions. The producer bivalve mollusc was not successive in its attempt at final escape and hence was trapped inside the burrow. The ripple cross-lamination that dominates the substrate containing the burrow and the immediately overlying sediment testifies to the relatively high-energy bottom conditions of this site. The various internal structures (i,e., V-shaped layering/spreite, digging core, and digging aureole) are well defined.

B. Inferred transverse cross-sectional views of the burrows at two different levels as defined in **A** (at A - B and X - Y) to illustrate the change from an eccentric to centric relationship of the digging core relative to the digging aureole with depth.

C. Idealized longitudinal cross-section of the burrow to illustrate the progressively more centric relationship of the digging core relative to the digging aureole with depth.





EXPLANATION

DC DIGGING CORE (core zone of sediment vertically bounded).

DA DIGGING AUREOLE (distance between two inflection points of a bedding-plane that has founded adjacent to the burrow).

COL CUT-OFF LAYER (inflection of founded bedding planes regardless of the direction of animal movement).

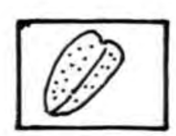
W WIDTH (diameter of the biconvex closed valves of the producer organism which approximates to DC & DA).

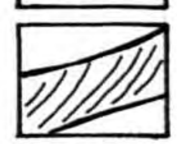
① Upward escape movement of the organism.

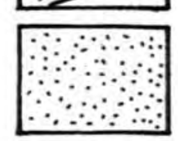
② Downward escape movement of the organism.

A ⊢-------⊣ B Upper cross-section.

X ⊢-------⊣ Y Lower cross-section.

 Infilled internal mould of the producer pelecypod in living position.

 Bedding and cross-stratification in very fine grained sandstones.

 Coarser sediment particles, mainly concentrated in DC & DA areas.

TEXT-FIG. 14.5.

by pulling and pushing movements of the foot. The animal's shell disrupts the surrounding strata along the escape path but the animal stops burrowing when it reaches a level from which it can reach the sediment-water interface with it's siphons and so remain safely buried from the activities of predators and strong currents on the surface. The organism has than to maintain that position (ultimate depth) beneath the sediment-water interface by periodic upwards and downwards adjustment as a consequence of deposition or erosion respectively. The escape-potential reconstructed from the depth of the burrows in the material from the study area shows that the bottom of all burrows is more than 5 cm from the reconstructed sediment-water interface and thus the producer bivalves are inferred to have been siphonate infaunal feeders (cf. Kranz, 1970). But in addition to depth, other controlling factors of their escape-potential cannot be ruled out, such as: (1) bivalve feeding group; (2) degree of mantle fusion; (3) siphon formation; (4) sediment types (5) level of energy of prevailing currents; (6) size of the bivalve mollusc and water temperature may also be involved but are probably of lesser importance than burrowing depth (see more details in Kranz, 1970).

The resulting structures produced by both modern and ancient bivalves in escaping their burrows reveals that these escape-structures appear in vertical sectional view as a nested series of V-shaped or inverted cones (Text-Fig. 14.5). In horizontal section or in surface plan (bedding-plane) view it is impossible to distinguish between a bivalve resting-trace and its escape-structure. Such differentiation can only be made on the basis of visual access to the structure in vertical (i.e., bedding-normal) section and resolution of the presence or absence of an escape-root (Text-Fig. 14.2).

The nested series of V-shaped layers that define the digging core and the digging aureole are readily discernable (Reineck, 1958) and are descrobed as follows (see also Text-Fig. 14.5).

Digging core (DC) (**WUHLKERN**): comprises the zone of sediment in the core of the burrow which roughly corresponds in diameter to the width of the bivalve mollusc with its valves closed. In some cases the coarser sediment (either from above or from the side of the burrow) can become concentrated in the digging core. These coarse sediment particles become concentrated through the beating movements of the bivalve's fleshy foot and by water discharge from its mantle cavity, the finer sediment particles being pushed or washed sideways into the interstices between sand grains.

Both the upward-pushing movements of the mollusc toward the surface and its downward-pulling movements loosen sandy or muddy sediment so much that the penetrated layers sag downward, in many cases quite some distance (regardless of whether the animal has moved up or down). The direction of deflection of the cut-off layers (Text-Fig. 14.5C) does not indicate the direction of movement of the animal (Schäfer, 1972). However, in the topo-type burrow the trapped pelecypod inhabitant is orientated in the escape orientation, that is in an orientation that places the anterior and dorsal margins diagonally uppermost and the posterior and ventral margins diagonally lowermost (cf. Text-Fig. 14.2) The digging core is not invariably layered but individual beds retain their identity across it if they are thicker than the height of the shell that penetrates them (cf. Text-Fig.14.2). The resulting sag-trails indicate the passage of a bivalve mollusc through the layered sediments. The digging core can shift towards the central area (axis of the burrow) when the animal descends deeper (Text-Figs. 14.5 B & C).

Digging aureole (DA) (**WUHLLOF**): The inflection point of the cut-off layers defines the digging aureole of the bivalve escape-burrow (cf. Text-Fig. 14.5C). If a digging trail is seen in vertical (longitudinal) section, beds in the aureole appear as simple sag-zones (sinkzones of weakness). The nearer the section coincides with the axis of the burrowing trail the deeper sag of the beds, and in this section both the digging aureole and the digging core can be recognized.

The texture and structure of the infill sediments were studied by Seilacher (1957) who interpreted them as comprising the concentrated coarser fraction of the host sediment along the tracks of the escaping bivalves. Actually, as mentioned already, the coarser grains have been separated from the initial host sediment by the beating movements of the foot of the bivalve and by water discharge from its mantle cavity. The finer grains are pushed or washed sideways into the surrounding sediments.

These bivalve escape-traces normally lack any features that are indicative of the individual species of the producer, and hence neither modern nor fossil traces can be used for comparative morphological studies. However, in rare cases in which the hard parts or the shell of the producer organism are preserved in living position inside the burrow (see Text-Fig. 14.5 and Plates 40 & 41), either at the end or at some other place along the escape-trail, then the biological identity of the producer organism is clear. The presence of the producer bivalve inside the escape-trail is quite unlikely because most dead bivalves (even where trapped inside the burrow) are at one time or another washed out and/or transported away from their last escape-burrows, at least in situation where the substrate is/was subject to frequent erosion. The chances of death are unequal on the upward and downward escape-paths. In the course of upward movement (normally during depositional episodes), the bivalve passes through successively younger and hence less firm or consolidated layers which are easier to penetrate the higher the organism ascends. In contrast, downward escape only leads the bivalve into firmer/more consolidated sediment through which it may no longer be able to burrow. Hence, the causes of death through entrapment in the burrow is more often likely to be erosion rather than sedimentation, but the importance of sudden excessive loading by new sediment cannot be discounted. The weight of suddenly added sediment can arrest movement by the organism and thus prevent it from regaining access to the sediment-water interface. It then dies in living position in its burrowing escape-trails (as in the case of one example in the present study area; see Text-Fig. 14.5 and Plates 40 & 41. The preservation of the escape-structure and the exoskeleton of the producer organism is more probable where thick layers of sediment are deposited quickly with only minor subsequent erosion. In the present study area heavy sedimentation was normally caused by a stream system that entered the area from the northwest or west and debauched into a coastal lagoon or estuary in the southeast (see Text-Fig. 5.2). This stream may have taken sediments from upstream and deposited them nearby in the lagoonal areas. But commonly the same sediment was probably retransported together with its contained infauna and with loss of the escape-trails. Also, traces of the living activities of bivalve molluscs are hardly preserved not because they are indistinct but because of the coarse texture of the sediment they commonly frequent and which does not readily preserve such details.

The majority of escape-traces of the form presently discussed here are believed to have been formed by siphonate infaunal bivalves on the basis of the relatively large depths of burrow penetration in the sediment, notwithstanding the fact that there are no preserved traces of pertubation texture produced by the siphons. During upward escape the muscular foot works to penetrate the soft sediment above the animal (see Text-Fig. 14.5 and Plates 40 & 41) in its attempts to reach the sediment-water interface. The pushing of the siphon can also loosen the sediment above and cause it to collapse into the escape-structure.

Comparison: Most fossil escape-structures produced by bivalve molluscs have been described under the ichnogeneric names Pelecypodichnus Seilacher, 1953 or Lockeia (James, 1879) (see Table 14.1) names were originally applied only to bivalve resting-traces as distinct from escape-traces. Numerous modern pelecypod escape-burrows have also been studied by Reineck (1958, 1967) and Schäfer (1972) but these workers did not use any ichnotaxonomic names in reference to them. I therefore believe it is appropriate and timely to erect a proper ichnotaxonomic terminology to accommodate the V-shaped escape-structures because of their different ethological origin to resting-traces and because of their distinctive structure. The present study specimens allows a good understanding of bivalve escape-burrows by virtue of their well preserved internal structures and in one case the fortunate circumstance of the producer bivalve mollusc having been trapped inside its burrow.

Studied material: The topotype specimen shown in Plates 40 and 41 and paratypes in Plate 42 are from logged section 14.1.1, of trace fossil subinterval IE1.1 of the Middle Newport Member at Mona Vale Head (area, 14) (see Text-Figs. 4.1 & 4.2).

Distribution: This type of bivalve escape-structure has been encountered only in trace fossil subinterval IE1.1 of the Middle Newport Member at Mona Vale Head (area 14). But similar resting traces of bivalves attributable to <u>Pelecypodichnus</u> Seilacher, 1953 or <u>Lockeia</u> (James, 1879) occur in underlying trace fossil subintervals ID5 and ID6 of the Lower Newport Member in the adjacent area at Bilgola Head (area 10). Pelecypod body fossils (one of which is illustrated in Plate 74, Fig. c) are also known from the lower part of Lower Newport Member (trace fossil subinterval ID1) at Warriewood Beach (area 6) (see also Grant-Mackie et al., 1985).

Preservation and association: These escape-structures are well preserved as full-relief forms in cross-laminated very fine to fine sandstone. This type of vertically orientated burrow with V-shaped internal layering is not associated with other types of vertical burrows.

Ichnofacies and palaeoenvironmental affinities: This kind of escape-structure belongs to the Skolithos ichnofacies and in the study area formed under the rapidly shoaling conditions of a river-influenced coastal lagoon or estuary.

A. alyxis ichno. sp. nov.

Plate 43, Figs. a - b

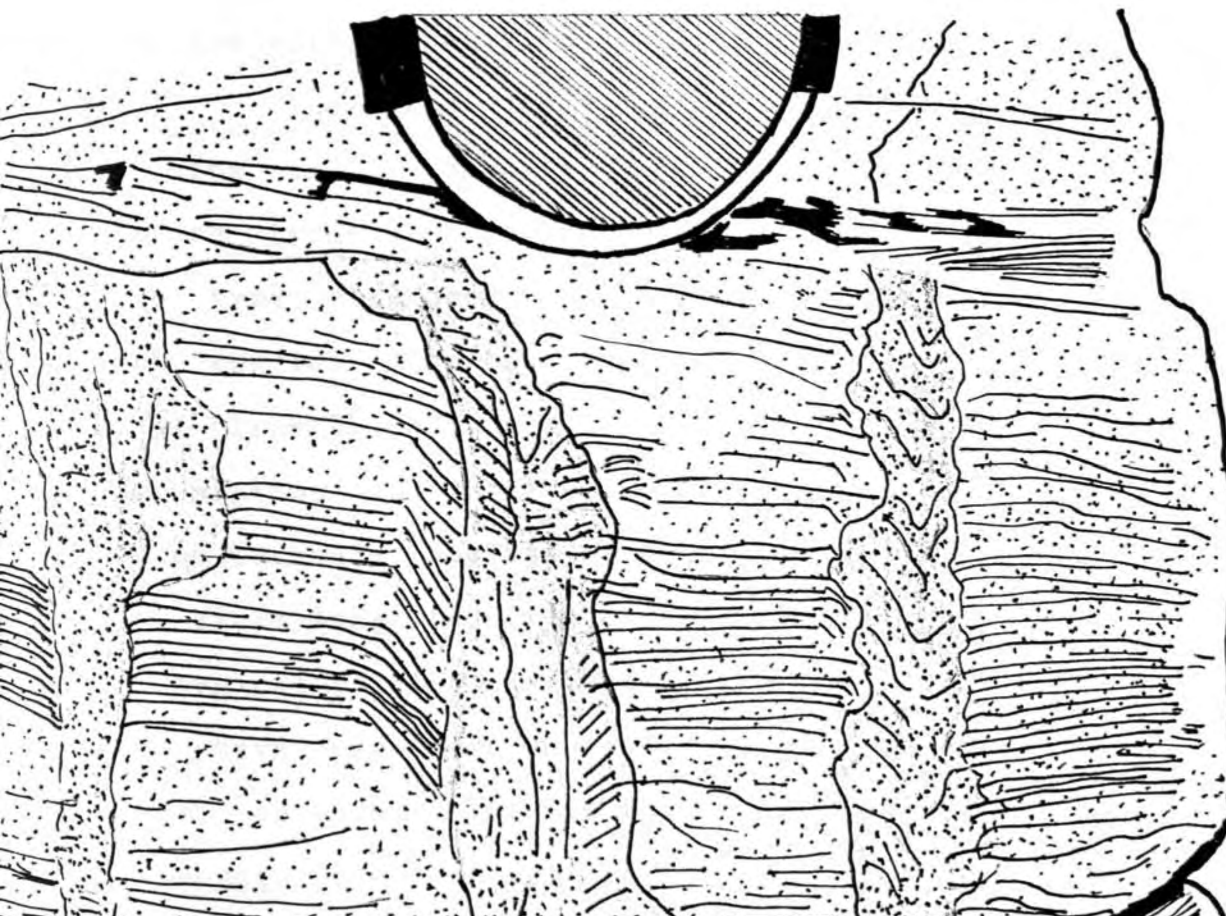
Derivation of name: `Alyxis' is a Greek word meaning `escape' or `free from'.

Diagnosis (specific assignment): Narrow vertical shaft with nested series of poorly defined V- or U-shaped layer/spreite constituting an escape-structures produced by a bivalve mollusc as a result of periodic unidirectional upward movements in order to escape burial and also to maintain a constant position relative to the sediment-water interface especially during episodes of bed accretion (Text-Fig. 14.1 & 14.6)

Remarks (diagnostic features): Narrow vertical shaft with nested series of poorly defined V- or U-shaped layer/spreite constituting an escape-structures (digging core and digging aureole are poorly defined, if present); other parts of the burrow are typically infilled with disturbed sediments. Typically occurs in parallel-laminated very fine sandstone and siltstone which reflect relatively slow accretion and hence a greater escape-potential of the producer bivalve.

Description and ethology: This type of bivalve mollusc escape-

TEXT-FIG. 14.6. Overlay sketch made from a photograph of the holotype (middle burrow) and paratypes (other two burrows) of the new ichnogenus Adeiaichnus alyxis (cf. Plate 43, Fig. b). These escape burrows belongs to the Type A variety 2 category in the present classification (cf. Text-Fig. 9.1), i,e., the category of simple vertical burrows characterized either by an absence of internal structures (e.g., burrow at left and lower part of middle burrow in this illustration) or by crudely defined V-shaped layering (e.g., upper part of middle burrow and burrow at right in this illustration). This kind of burrow was evidently formed by organisms that were forced to move consistently upward in order to escape burial and to maintain a constant position relative to the sediment-water interface under conditions of progressive accretion on the bed. In comparison with the type species (i.e., A. kykleomotatus , cf. Text-Fig. 14.1 and 14.5) the producer bivalve molluscs were successful in escaping their burrows. The parallel-lamination of the host siltstone testifies to the relatively slower rates of bed accretion at this site and hence the relatively greater ease escape compared to A. kykleomotatus. Definition of the internal structures (V-shaped layering/spreite, digging core, and digging aureole) are not as well defined as in the type species even where present. Scale: 5 cm diameter lens cap.



ESCAPE-STRUCTURES (TYPE A VARIETY 2)
(RAPID ESCAPE).

TEXT-FIG. 14.6.

structure is characterized by poorly defined burrow trails along the escape-passage (Text-Figs. 14.1 & 14.6). The width of is traces is 2 cm to 3 cm and the depth of the shaft about 10 cm as measured from the reconstructed sediment-water interface. Most of the internal structures are poorly defined and hardly discernible; V- or U-shaped traces do occur in some examples but are asymmetrical (Text-Fig. 14.6). This type of escape-burrow is commonly made by bivalve molluscs but it is referred here to a species different to A. kykleomotatus because it manifests a different ethology (behavior) to the latter.

The burrow was established by the same types of bivalve molluscs as in the case of the type species (i.e., siphonate feeding types with escape-potential in excess of 5 cm) and the same types of procedures for starting the burrow hold as in the type species. The organism stops burrowing when it attains a level from which it can reach the sediment-water interface with its siphons and where it is safe from predators and strong bottom currents. Because of the slower rates of bed accretion at the sites inhabited by the producer pelecypod (as indicated by the typical parallel-laminated structure of these substrates) it must have been mere sensitive to the need for more continuous upward adjustment of its burial depth than in the case of A. kykleomotatus which reflects more episodic upward and downward movement because of the inferred less stable bottom conditions which evidently applied in its case. Thus, in A. alyxis the escape-trail is established only by one-directional (upward) movement of the pelecypod and as a result the internal structures are not as well defined as in the case of the A. kykleomotatus. V- or

U-shaped internal layering does exist in some places in some of these escape-burrows but they are asymmetrical and not well defined (Text-Fig. 14.6). Spreite, digging core, and digging aureole are not readily discernible in many cases and even where they are the definition of their boundaries is diffuse. In some cases the digging aureole may be defined where cut-off layers are well preserved (Text-Fig. 14.6). The digging core tends to change from being eccentric in the upper part of the burrow to being centric in the lower parts in examples from the study area (cf. Text-Fig. 14.5) but this pattern is not as well defined as in the case of A. kykleomotatus.

The texture and composition of the sediment infilling the core zone of the burrow is the same as the surrounding host sediment and there is no actual concentration of coarser grains in this core zone. This infilling sediment is derived mainly from above and to the sides of the burrow.

The presence of the producer bivalve inside the escape-trail in A. alyxis is quite unlikely because the chances of it being trapped inside the burrow is less than in the case of the type species. Moreover, the occurrence of this kind of escape-burrow exclusively in parallel-laminated fine-grained sediment indicates that bed accretion rates were probably mainly relatively slow, thus enhancing the animal's chances of escape. If the pelecypod could move fairly rapidly upwards to maintain its position relative to the sediment-water interface, its chances of escaping burial during intervals of more rapid bed accretion would be good. In the absence of erosional episodes the pelecypod has no reason to move downwards to a depth that may lead to its burial and death inside the burrow. Also, in the absence of strong bottom erosion the preservation potential of the escape-burrow would be high.

The burrows of A. alyxis are also believed to have been produced by siphonate feeding pelecypods (as in the case of the type species), but the burrow infills lack the concentration of coarser sediment typical of the type species and are more disturbed than in the type species. Again, it is not possible to discount totally the possibility that this disturbance has been produced by sediment pertubation by the animal's siphon. One possible explanation is that movement of the siphons loosens the sediment above and causes it to collapse into the burrow below; a second possibility is that currents exhaled by the siphon at the posterior margin of the bivalve may cause all of this sediment disturbances.

Comparison: This new species occurs in trace fossil subinterval IE1.2 immediately above that in which the type species was discovered. As in the case of the type species, these structures are also believed to have been produced by bivalve molluscs but involving more rapid escape than in the case of the type species. The sizes and depths of the two varieties of burrows are quite comparable. No previously studied specimens are quite comparable with these newly described species (see Table 14.2).

Studied materials: The specific topotype specimen is chosen from the illustration shown in Plate 43 Fig. b, and the paratypes are from Plate 43 Fig. a, and Plate 44, Fig. a. All photographs were taken within trace fossil subinterval IE1.2 in the lower horizons of the Middle Newport Member at Mona Vale Head (area 14) (see Text-Figs. 4.1 & 4.2).

Distribution: This new species occurs in trace fossil subinterval IE1.2 (above the horizon containing the type species in subinterval IE1.1) of the lower horizons of the Middle Newport Member at Mona Vale Head (area 14). The known distribution is limited to that area and that particular horizon (Text.Figs. 14.1, 14.2 and Enclosure III.2).

Preservation and association: These narrow vertical shafts characterized by poorly defined V-shaped bivalve escape-structure are well preserved as full-relief forms in parallel-laminated very fine sandstone and siltstone. These structures are not associated with any other types of vertical burrows or any other kinds of trace fossils.

Ichnofacies and palaeoenvironmental affinities: These pelecypod escape-structures are most common in the Skolithos ichnofacies and in the study area formed in the depositional setting of a river-influenced coastal lagoon or estuary.

Hannibalichnus ichno. gen. nov.

Chagrinichnites osgoodi Hannibal & Feldmann; Hannibal & Feldmann, 1983, p. 710, figs. 4A, B, & C.

Type ichnospecies Hannibalichnus osgoodi (Hannibal & Feldmann, 1983).

Derivation of name: In honor of J. T. Hannibal, who described the first arthropod escape-trails.

Diagnosis (generic assignment): As seen in vertical transverse cross-section, the burrow is a large W-shaped, bilaterally symmetrical escape-trace produced by an arthropod or fish or possibly by an amphibian.

Diagnostic features: As seen in vertical transverse cross-section, the burrow is a large bilaterally symmetrical W-shaped or bilobed escape-trace, typically with depressed lateral regions separated by a broad raised medial ridge (Text-Figs. 14.1 and 14.7). No transition to a resting-trace (rusophysiform) or crawling-trace (cruzianiform) is present (cf. Text-Fig. 14.4). A collapse-structure occurs immediately above (Text-Fig. 14.1 & 14.7).

H. amplius ichno. sp. nov.

Plate 44, Fig. b (monotypic)

Derivation of name: From the French word, 'Amplius' meaning 'larger'.

Diagnosis (specific assignment): Large bilaterally symmetrical W-shaped (bilobed) escape-structure (as seen in vertical transverse cross-section), typified by its broad bilobed depressed lateral areas that are separated by a longitudinal medial ridge (Text-Fig. 14.1).

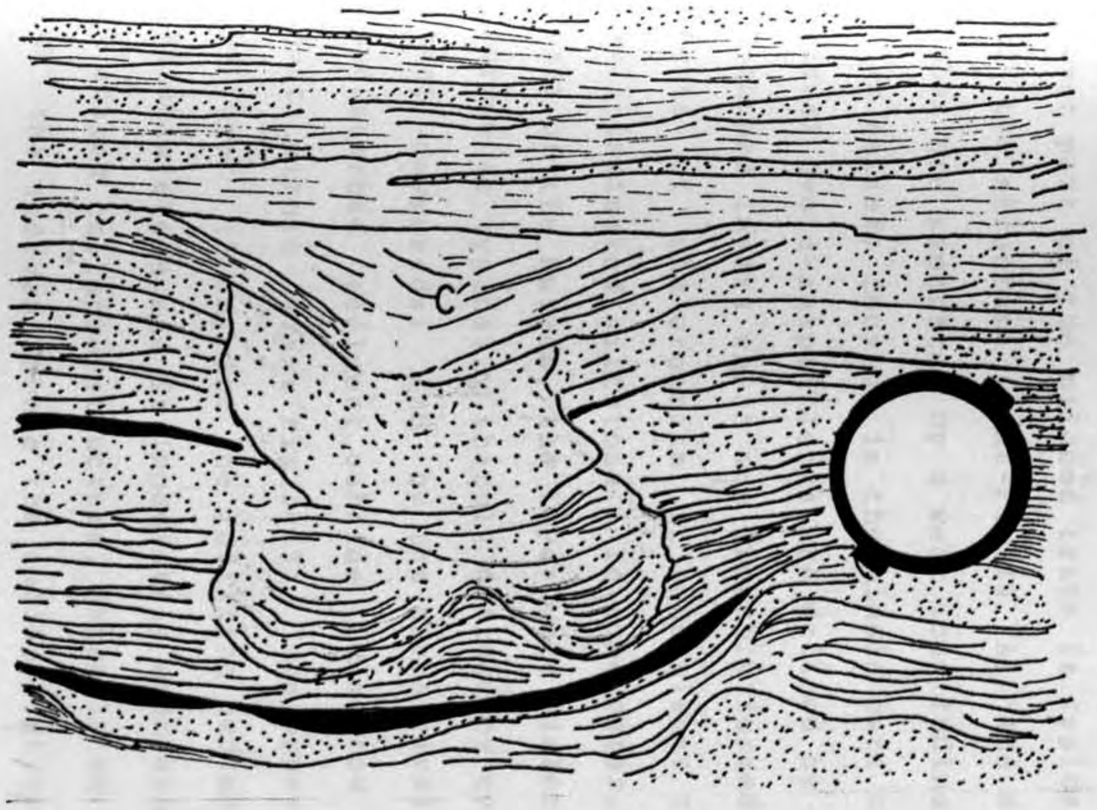
Diagnostic features: As seen in vertical transverse cross-section the burrow is a large, bilaterally symmetrical bilobed escape-trace. The internal structure consists of a series of nested broad U-shaped layers developed within each of the lobes becoming W-shaped where they connect across the medial ridge (Text-Figs 14.3 & 14.7). No indication of the producing animals appendages or any other details of it apart from the bilobed form a preserved in the example studied. The burrow is not associated with crawling (cruzianiform) traces and there is no indication of a

TEXT-FIG. 14.7. A. Overlay sketch made from a photograph of the topotype of the new ichnogenus Hannibalichnus amplius (cf. Plate 44, Fig. b). This escape-burrow belongs to the type B category in the present classification (cf. Fig. 14.1), i.e., the category of bilobed escape-burrows with internal W-shaped layering. This kind of burrow was produced either by an arthropod or a fish, or possibly by an amphibian that lay shallowly buried by sand in a shallow resting burrow but which was forced to move progressively upwards to escape complete burial due to accretion of the substrate (cf. Text-Fig. 14.3). This kind of escape burrow is invariably overlain by a collapse structure (C) and passes obliquely downwards into a resting structure (cf. Text-Fig. 14.3).

C and D. The same overlay sketch as in **A** but with hypothetical reconstructions of the likely producing organisms. i.e., an arthropod (in **B**) and a fish (in **C**).

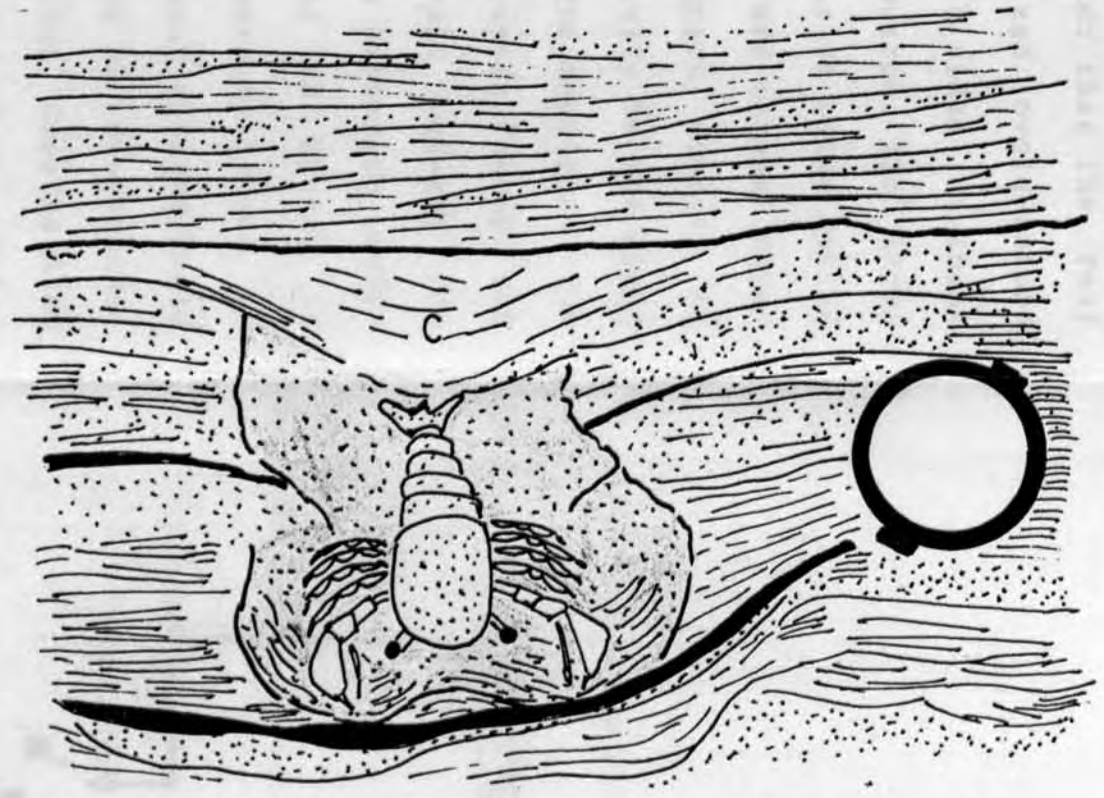
Scale: 5 cm diameter lens cap.

A



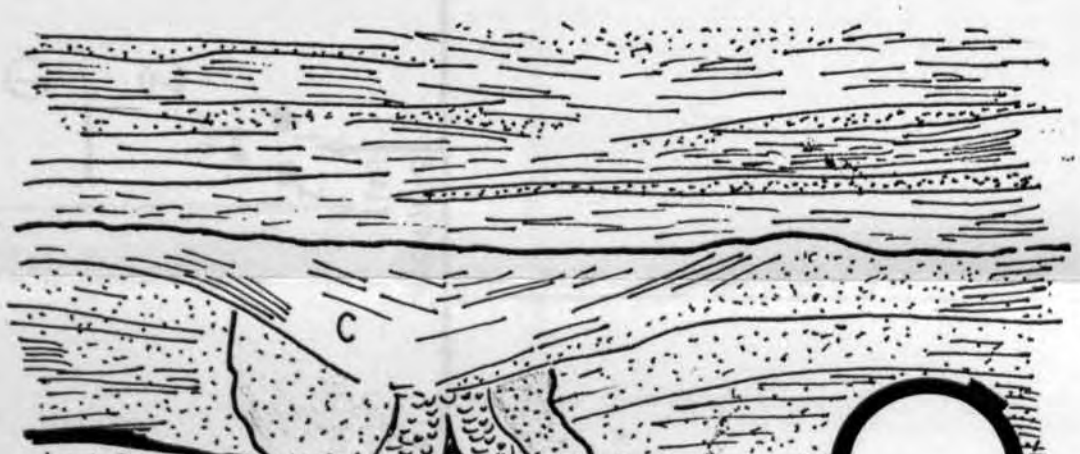
ESCAPE-STRUCTURE. (TYPE B).

B



INTERPRETATION. 1. PRODUCED BY CRUSTACEAN.

C



INTERPRETATION 2. PRODUCED BY FISH.

(C = COLLAPSE-STRUCTURE)

TEXT-FIG. 14.7.

resting (rusophyciform) trace at the bottom of the burrow. A broad V-shaped collapse-structure is present immediately above the burrow (Text-Figs. 14.3 & 14.7).

Description and ethology: This new ichnospecies is a large (10 cm width by 5 cm depth and length presently unknown - collapse-structure not included), bilaterally symmetrical trace with full-relief preservation in parallel-laminated siltstone and very fine sandstone. As seen in vertical transverse cross-section the lower part of the bilobed trace is typically wider than the rest of the structure (Text-Fig.14.7A). The equal-sized ovoid-shaped lobes are separated by a weak longitudinal medial ridge (of about 1 cm relief) located in the middle part of the burrow. The individual ovoid-shaped lobes are defined by a series of broad nested U-shaped layers which are probably formed by upward escape movements of the organism; in some places these layers consist of well-laminated siltstone . In some cases, especially in the upper part of the burrow, the layers are distorted . The margin of the burrow is typically sharply defined by cut-off layers (abrupt and bent downwards) and by the geometrical contrast between the undisturbed sediment outside the burrow and the disturbed sediment within (Text Fig.14.7). The upper part of the burrow is narrower (8 cm) and the infilling sediment is more disturbed or structureless and is immediately overlain by a well defined broad V-shaped collapse-structure. There is no evidence of disturbance of the sediment above the collapse-structure thus constraining the timing of the animal's escape prior to the time of deposition of the former.

No skeletal remains of the producer organism(s) or any other direct evidence of it that might lead to its identification is available in the studied example. Nevertheless, this type of bilobed escape-structure can be explained by reference to at least two different types of organisms (see Text-Figs. 14.7B & C). Thus, the structure may have been produced by the escaping behavior either of an arthropod or a fish. The possibility that it was produced by an amphibian also cannot be discounted.

In this interpretation an arthropod (crustacean) or a fish was resting by partly burrowing in the silt substrate, this substrate reflecting low-energy conditions. The site was then quickly blanketed by a comparatively thick layer of very fine sand and silt. Thus, the organism was progressively and temporarily buried under these new sediments which it tried to shed by periodic upward movement until it finally made an actual escape. Its escape was then followed by collapse of the sediments overlying the escape-burrow (cf. Text.Fig. 14.3).

Comparison: The new species, H. amplius, is distinctly larger than the type specimen described by Hannibal & Feldmann (1983). The association of the resting-trace (rusophyciform) Chagrinichnites brooksi Feldmann et al. (1978) is not demonstrable in the study specimen. But theoretically the resting-trace may be found at the bottom of the escape-trace (see Text-Figs. 14.3 & 14.4 for definition of the taxonomic boundary). A transition with a crawling-trace (cruzianiform) is also not demonstrable in the present example studied. The other related structures discussed by Hannibal & Fieldmann (1983) for comparison with H. osgoodi are mainly arthropod resting-structures rather than escape-structure.

Studied material: The monotypic specimen occurs in situ in trace fossil subinterval ID2.5 of logged section 5.1.1 in the Lower Newport Member at St. Michaels Cave (area 5). The specimen has not been retrieved from the field.

Distribution: The specimen occurs in trace fossil subinterval ID2.5 within the Lower Newport Member at St. Michaels cave (area 5). The structure has a broad V-shaped collapse-structure at the top of the escape-trail. Similar broad V-shaped collapse-structures are common in the adjacent areas of Bangalley Head (in the north, area 8) and Hole in the Wall (in the south, area 11) where the same stratigraphic unit is exposed. However, no escape-burrows of any kind are evident in association with these latter collapse-structures although the explanation of their absence is unclear.

Preservation and association: This structure is preserved as a positive bilobed full-relief form and overlain by a broad collapse-structure. Collapse-structures of the latter kind are commonly associated with the star-shaped new ichnogenus Helikospirichnus (discussed in the Chapter 8).

Ichnofacies and palaeoenvironmental affinities: In the study area this escape-structure occurs within the Skolithos ichnofacies which probably formed in the shallow-waters of a riverine brackish-marine coastal lagoon or estuary (see Text-Fig. 5.2). The ichnospecies H. osgoodi (Hannibal & Feldmann, 1983), the type species, is indicative of storm deposits as inferred by Hannibal and Fieldmann from the Chagrin Shales (Upper Devonian) of Ohio, USA.

Collapse-structures

Plate 44, Fig. b
Plate 78, Fig. e

In the study area collapse-structures comprises vertical successions of down-bent laminae, usually associated with the star-shaped traces of <u>Helikospirichnus veeversi</u> ichno. gen. sp. nov. (Plates. 45 - 47), and the arthropod/fish escape-structure <u>Hannibalichnus amplius</u> ichno. gen. sp. nov. They occur immediately above the vacant burrows, manifesting the collapse of the latter and their infilling with sediment. Collapse-structures are not true trace fossils, because they do not directly manifest the behavior of an organism, but are instead indirectly created by an organism (see Text-Fig. 9.7, & Plate 44, Fig. b).

Collapse-structures are sometimes confused with escape-traces (Plates 40 - 44); but they differ from the latter in regard to the inclination of the laminae and the texture of the infilling sediment. The inclination of the laminae in collapse-structures decreases upward. In contrast, laminae in escape-structures generally exhibit a uniform inclination vertically. Escape-traces are often cast by overlying sediments whereas collapse-structures are commonly infilled with overlying and laterally adjacent sediments.

In the study area these collapse-structures are known only from the Middle Newport Formation at Bangalley Head, St. Michaels Cave and the Hole in the Wall areas and are especially common at the latter locality.