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THE CAMBRIAN LOBOPODIAN *MICRODICTYON SINICUM*

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ABSTRACT—*Microdictyon* was a soft-bodied onychophoran-like animal, forming a significant component in many Early Cambrian faunas. It was for long known only from disarticulated, mineralized plates. The discovery of the first complete specimens of *Microdictyon* (Chen *et al.* 1989) unexpectedly showed that such plates attached to the trunk sides of a caterpillar-like animal. About 70 new specimens recently collected permit a detailed and more comprehensive description of *Microdictyon sinicum* than could be accomplished in the original paper. Homology analyses favor a reinterpretation of *Microdictyon sincium,* with a reversal of the first suggested anteroposterior orientation. In the new reconstruction, this animal had a long, weakly tapering anterior extension (head) with a terminal mouth, and an annulated, subcylindrical trunk which was supported on ten pairs of annulated legs bearing paired claws; posteriorly was a short anal extension. Along its flanks, there were nine pairs of tough, possibly mineralized plates. The presence in many specimens of double sets of plates, with one set 13-20% larger than the other, shows that before molting the new plates were formed beneath the old ones. Small *Microdictyon* specimens are usually in direct association with *Eldonia,* a pelagic animal, which indicates a pseudopelagic life style in juveniles. Closest affinity of this unusual animal lies with the celebrated *Hallucigenia* and other armoured lobopodians, together forming a group closely allied with the Recent Onychophora. The relationships between the two groups are left undetermined pending a detailed phylogenetic analysis.

KEY WORDS: *Microdictyon,* lobopodian, Cambrian explosion, Chengjiang, evolution

INTRODUCTION

The fossil record is a biased sample of the history of life. The majority of early organisms were soft bodied, and under normal circumstances they would not be fossilized or leave any trace in the rocks, and they were therefore destined never to be known to science. Some members of the marine, soft-bodied fauna bore internal or external, mineralized plates which dispersed when the individual died. The plates could also pass intact through the gut of predators. If embedded and preserved in the sea bottom sediments, they could leave a record for posterity. The fossil plates provide limited clues to the identity of the animals that carried them and to their original distribution over part or all of the external body (Conway Morris, 1992), which has been a matter of much puzzling and controversy in science.

A research field of special interest is that of Lagerstätten, i.e., the occurrences of extraordinary preservation, particularly of soft body parts besides mineralized hard parts. These occurrences provide a much more complete information of early life than the ordinary localities, yielding only the mineralized parts. In Cambrian faunas, Lagerstätten with soft-body preservation reveal that only a small fraction of the fauna is preserved under normal circumstances (Conway Morris, 1986). The Chengjiang Lagerstätte from Chengjiang, E. Yunna (Text-fig. 1), was discovered in 1984 and is noted as one of the world's most important fossil occurrences (see Chen *et al.*, 1991; Chen and Erdtmann, 1991). It not only shows superb soft-bodied preservation, but its overriding importance lies with the age of the biota, because the organisms

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represented in these rocks lived during the early stages of metazoan life, a gigantic leap in diversification of life known as the "Cambrian Explosion" (e.g. Conway Morris, 1992). This is when the first complex marine life appeared and proliferated on Earth (e.g., Levinton, 1992).

The Cambrian period was for long known as the "Age of Trilobites", but this type of animal represents only 3% of the species in the Chengjiang fauna and much less in terms of the number of individuals. This fact highlights the importance of the Chengjiang fauna in the understanding of the evolution of early life, of which we still know but tiny patches. Most early work on the Chengjiang fauna concentrated on taxonomic descriptions, including papers published by Zhang (1987), Zhang and Hou (1985), Hou (1987a, b, c and d), Hou and Chen (1989), Hou *et al.* (1991), Hou and Bergström (1991), Sun and Hou (1987a, b); Chen *et al.* (1989a, b and c; 1990), Chen and Erdtmann (1991), Chen *et al.* (1991), Jin *et al.* (1993), and Chen *et al.* (1995). Phylogenetic aspects of Chengjiang taxa have more recently begun to be studied, in particular by Ramsköld and Hou (1991), Ramsköld (1992b), Hou and Bergström (1994), Chen *et al.* (1994), and Chen *et al.* (in press).

The *Microdictyon* animal left its wide-spread record in the Cambrian rocks with its mineralized shoulder plates. For these isolated plates, extracted from the rock with the use of acid dissolving the rock and leaving isolated mineralized small fossils, the generic name *Microdictyon* was introduced in 1981 by Bengtson, Matthews and Missarzhevsky (in Missarzhevsky and Mambetov, 1981). Several species have been erected since 1981 by the following authors: Bengtson, Matthews and Missarzhevsky (1986), Hinz (1987); Tong (1989); and Bengtson *et al.* (1990). Because the plates in *Microdictyon* are preserved as phosphatic shells, all described material comes from acid residues, and the genus has been reported from Lower and Middle Cambrian carbonate rocks in Siberia, Kazakhstan, England, Sweden, Denmark, Australia, Mexico, USA and Canada (see Bengtson *et al.*, 1986 for locality data and references; for Mexico also McMenamin and McMenamin, 1990; and for Australia Bengtson *et al.*, 1990). *Microdictyon* has also been described from China (Tong, 1989), although incorrectly recognized as radiolarian tests in the first descriptions (Hao and Shu, 1987; Shu and Chen, 1988). With their striking shape, *Microdictyon* plates have attracted considerable attention from researchers attempting to understand the underlying biology, but without knowledge of the soft parts of the *Microdictyon* animal, the earlier attempts failed.

Complete specimens of the entire animal, including the soft tissues, were first described in 1989 by Chen, Hou and Lu, and are known only from the Chengjiang Lagerstätte. The discovery of complete specimens proves that *Microdictyon* was a soft bodied caterpillar-like animal, with large adults reaching 50-75 mm in extended length, showing paired lobopod limbs. It was unexpectedly realized that the intricately shaped plates were positioned along the sides of the body, which is so morphologically similar to the living Onychophora, or velvet worms, that *Microdictyon* was allied with that phylum by Ramsköld and Hou (1991).

Over 70 new specimens have been collected between 1990 and 1994. Almost all specimens (excluding only some poor or uniformative ones) have been included in the present study and have been carefully prepared to uncover parts which were covered by matrix. A large number of specimens are illustrated here by photographs and interpreted in camera lucida drawings, some of which combine information from both part and counterpart.

Although the anatomy favors a lateral preservation, a number of specimens show the animal preserved in other positions, including specimens with their dorsum facing upward. All well preserved specimens show traces of the gut, indicating that they are not molts but dead individuals, and it appears probable that most of the animals were alive when transported in the turbidites carrying them to their burial ground.

A substantial increase in new material together with a major improvement in the effort for detailed preparation allows for the first time a detailed and reasonably definite description of *Microdictyon sinicum*. New morphological evidence and anatomical analysis indicate close ties to the fossil forms; *Hallucigenia* (Conway Morris, 1977; see Ramsköld, 1992a), *Xenusion* (Pompeckj, 1927: see Dzik and Krumbiegel, 1989), *Luolishania* (Hou and Chen, 1989), *Aysheaia* (Walcott, 1911; see Whittington, 1978), *Onychodictyon* and *Cardiodictyon* (Ramsköld and Hou, 1991; Hou *et al.*, 1991), and *Paucipodia nomen nudum* (Chen, Zhou and Ramsköld, 1995). These lobopodian worms are marine organisms and share a number of important features, suggesting that they are closely related, forming a monophyletic group. Their head region is not distinctly separated from rest of the body, and the similarities to the extant terrestrial Onychophora are striking. Significant differences between the fossil lobopodians and the living, terrestrial onychophorans are present in the head region, in that the fossil forms have a terminal, apparently jawless mouth and lack the pair of antennae present in extant onychophorans.

The present study of one important member of this recently discovered group of extinct, marine lobopodian worms indicates that they may have possessed a less complex body design than Recent lobopodian organisms, including onychophorans and tardigrades. This, together with their living during the earliest phases of metazoan diversification, might be thought to suggest that they could be ancestral to some of the extant 'uniramian' organisms, and thus forming a paraphyletic group. However, they display a number of obviously apomorphic (advanced) characters, such as the presence of paired plates along the sides of the trunk. These characters make it appear more probable that they represent a separate branch of evolution than an ancestral (and thus paraphyletic) group. The relationships of this group to the Recent lobopodian groups Onychophora and Tardigrada are discussed comprehensively in a separate study (Ramsköld and Chen, in prep.).

MATERIAL

The specimens under present study include: the type specimens, NIGP 108286 (holotype); 108287, 108288, 108289, 108290, 108291, 108292, 108293, 108297, 108294-108296, plus six other specimens (then unnumbered) which were illustrated by Chen *et al.* (1989a). NIGP 108286 and 108287 are laterally compacted specimens of entire animals, which have been excavated recently by one of the authors to uncover the concealed parts of the body. NIGP 108289, 108290, 108291, 108292, 108293 are obliquely or subdorsally compacted, representing animals which were buried in a life position. Also NIGP 108289 has recently been excavated to uncover concealed parts. A group of seven juvenile *Micordictyon* specimens is present on the surface of a single *Eldonia* body. Only three of these individuals were previously recognized and provided with NIGP numbers 108294-108296. Except for the following six specimens: NIGP 108288, 108290-108293 and 108297, all the type specimens are illustrated and described in the present paper.

The type specimens previously illustrated by Chen *et al.* (1989a) are housed in the Nanjing Institute of Geology & Palaeontology (prefixed NIGP). In addition there are some 70 specimens collected since the winter of 1990. These are housed in the Museum of the Early Life Research Center (prefixed ELRC) and provided with the numbers 30001-30065. The following list indicates presence of counterpart (a, b), locality, orientation and completeness, and plate references:

30001a, b. MN5, lateral compaction (pl. 12, fig. 1);
30002, MQ1, fragment (not figured);
30003, MQ1, fragment (not figured);
30004, MN6, fragment (not figured);
30005, MQ1, sublateral specimen (pl. 20, fig. 2);
30006a, b, MQ1, lateral specimen (pl. 19, figs. 1-2);
30007a, b, MQ1, sublateral specimen (pl. 6, fig. 1);
3008, MQ1, lateral specimen (pl. 10, fig. 2; pl. 11, fig. 2);
30009, MQ1, lateral specimen (pl. 13, fig. 2);
30010, MQ1, posterior portion (pl. 17, fig. 2);
30011, MN6, subdorsally compacted specimen (pl. 17, fig. 1);
30012, MN5, subdorsal specimen (pl. 2, figs. 1-2; pl. 3, fig. 2);
30013, MQA, sublateral specimen, attaching to an *Eldonia* (not figured);
30014, MQ1, fragment (not figured);
30015, MQ1, lateral specimen (pl. 18, fig. 2);
30016, MQ1, lateral specimen (pl. 12, fig. 2);
30017, MN5, sublateral specimen (pl. 11, fig. 1);
30018a, b, MQ1, associated with *Eldonia* (not figured);
30021a, b, MN5, lateral specimen (pl. 16, figs. 1-2);
30022, MQA, subdorsal preservation (pl. 14, fig. 2);
30023, MQ1, fragment (not figured);
30024, MQ1, fragment (not figured);
30026, MQ1, fragment, subdorsal specimen (not figured);
30027a, b, MQ1, lateral specimen (pl. 9, figs. 1-2);
30028, MQ1, fragment (not figured);
30030, MQ1, fragment (not figured);
30031, MQA, subdorsal compaction (pl. 15, fig. 1);
30032, MQ1, a single plate (not figured);
30033, MQ1, subdorsal compaction (pl. 13, fig. 1, left);
30034, MQ1, subdorsal compaction (pl. 13, fig. 1,

right);
30035, MQA, fragment (not figured);
30036a, b, MQA, subdorsal specimen (pl. 16, figs. 3-4);
30039, MQA, fragment (pl. 10, fig. 1, left);
30040, MQA, fragment (pl. 10, fig. 1, right);
30041, MQA, subdorsal specimen (pl. 10, fig. 1, middle);
30042a, b, MQA, subdorsal specimen, co-occuring with an arthropod (pl. 20, fig. 1);
30044, MQA (not figured);
30045a, b, MQA, attaching to an *Eldonia* (pl. 1, fig. 2);
30046a, b, MQA, associated with *Eldonia* (pl. 14, fig. 1);
30047, MQA (not figured);
30049a, b, MQA, subdorsal specimen (pl. 8, figs. 1-3);
30051, MQ1, subdorsal compaction (pl. 18, fig. 1);
30052, MQ1, nearly complete (not figured);
30053, MQ1, an anterior portion (not figured);
30054, MQ1, fragment (not figured);
30055, MN5, fragment (not figured);
30056, MQ1, fragment (not figured);
30057, MN5, fragment (not figured);
30058, MQ1, subdorsal compaction (pl. 7, fig. 1);
30060, MN5, associated with *Eldonia* (pl. 5, fig. 2; pl.6, fig. 2);
30061, MQ1, lateral specimen (pl. 15, fig. 2);
30062-30065, M2, associated with an *Eldonia* (pl. 3, fig. 1; pl. 4).

We have also studied the seven well-preserved specimens collected by Sun Weiguo and the material collected by Hou Xianguang. These specimens are not illustrated or described in this paper.

METHODS

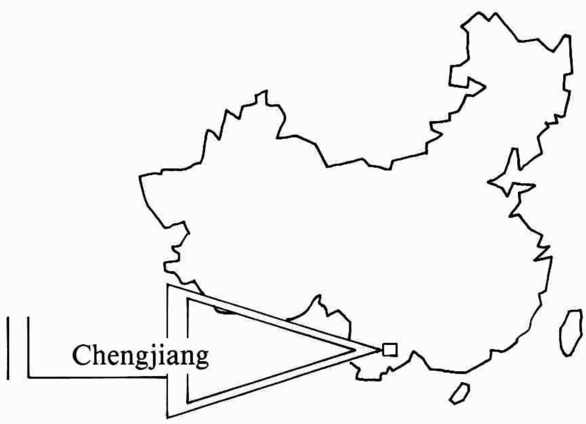
The specimens are not mere flattened sheets but most of them are three-dimensional and incompletely exposed, so skill and patience is needed for successful preparation of the specimens (executed by Z. G.-q. and L. R.) in order to reveal fine detail for extraction of maximum amount of information. Specimens were prepared under a binocular microscope with the aid of the tip of a scalpel blade to flake off either the matrix or the overlying parts of a specimen to reveal areas concealed below. A vibrotool became available when L. R. conducted work at the Early Life Research Center during the final phases of this study, and it proved efficient both for large scale removal of matrix and for fine detailed preparation. There is usually a weak zone between the fossil and the matrix, but since the surface of the fossils is commonly preserved as a reddish film with irregular surface, the soft rock matrix will usually not part cleanly from the fossil but very small chips of matrix must be removed until the surface is exposed. An air blower was used to remove dust during preparation. All the photographs illustrated in this paper are of dry specimens and were made at low or medium angle reflected light.

Camera lucida drawings are extensively used in this study to convey the authors' interpretation of the specimens, and an artists impression of how the *Microdictyon* animals could have appeared in life is presented (Text-fig. 7).

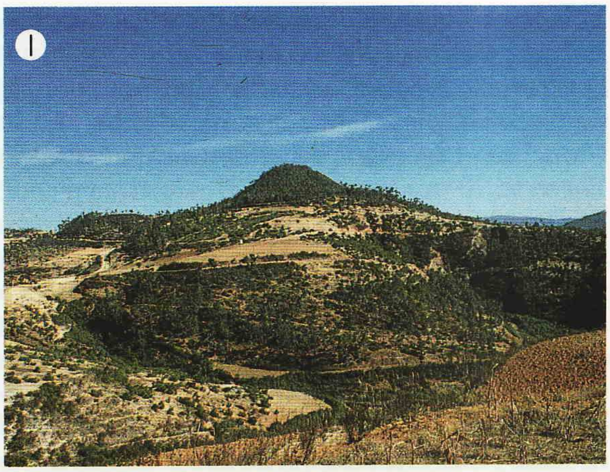
LOCALITIES AND STRATIGRAPHY

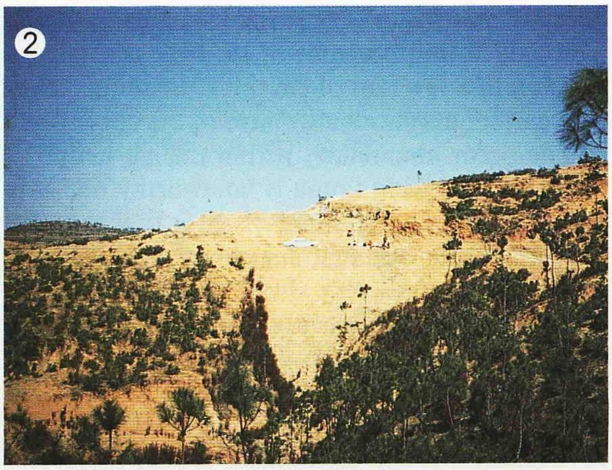
The area yielding the Chengjiang fossil fauna has received international acclaim as an area of paramount importance to our knowledge of early life (Conway Morris 1990a, b, 1992; Gould, 1993). It lies six kilometres E of the town of Chengjiang county, eastern Yunnan (Text-fig. 1).

On the west facing slope of Mt. Maotian, at an elevation of about 1984-1988 m, several quarries cut into gently dipping Lower Cambrian strata yielding one of the most significant fossil faunas ever discovered. The specimens of *Microdictyon sinicum* are collected mainly on the southwestern slope of Mt. Maotian (Text-fig. 2), from two separate quarries referred to here as MQ1 and MQA. The



Text-figure 1. Map of China showing position of the Chengjiang fossil Lagerstätte, Chengjiang, Yunnan, south China.





Text-figure 2. View toward the south-facing slope of Mt. Maotian (1) and a closer view of the south-facing slope of Mt. Maotian, showing excavation being carried out on the fossil sites MQ1 and MQA in the early spring of 1991 (photograph by D. Collins) (2).

quarry MQ1 is the classical quarry of the Chengjiang Lagerstätte, situated along the uphill side of a road (connecting a phosphate mill and its water pump room). The quarry was measured in 1992, and a coordinate system was established, with the base of a turbidite sand bed in the middle part of this section as the zero level. *Microdictyon* mainly come from an *Eldonia*-bearing, thin mud bed lying at -1.18 m. This quarry cuts into an about 5-6m thick, gently dipping sequence belonging to the lower part of the Yu'anshan Member, the upper unit of the Qiongzhusi Formation. The Yu'anshan Member in the Mt. Maotian area was previously named the Maotianshan Shale by Ho (1942), and in later publications most authors preferred to refer to it as the Yuanshan Member (Lu & Zhu, 1981; Zhang, 1987; Hou, 1987a-d; Chen *et al.*, 1989a; Luo *et al.*, 1982). The total thickness of the Yu'anshan Member is difficult to estimate due to frequent faults, but is at least 150 m, possibly up to 230 m (Zhang, 1987). The Member is divided into the following two trilobite zones: the *Parabadiella* Zone occurring in the upper 3 m of the 20 m thick basal black shale (the underlying part being largely unfossiliferous and unassigned to any Zone), and the *Eoredlichia* Zone extending throughout the Yu'anshan Member with the exception of its basal black shale. The stratigraphic unit in MQ1 lies some 20 m above the base of the *Eoredlichia* Zone, that is, within the lower part of the Zone. The quarry MQA lies some 10 to 20 m north of MQ1, exposing a 4-5 m thick sequence of strata representing a stratigraphic level lying immediately underneath that of MQ1.

The Yu'anshan Member extends to the north, having a broad exposure on the NW-facing slope of Mt. Maotian. From there several specimens of *Microdictyon* were collected in the summer of 1992 when a large scale bulldozer operation took place for the construction of a new road which passes along the north flank of the Mt. Maotian. The fossils were collected from a stratigraphic interval of about 5-7 m representing roughly the same stratigraphic interval as that at MQ1. This locality is referred to as MN and provided with numbers from 1 to 6 referring to the levels, in a stratigraphically ascending order, from which the fossil(s) were collected.

PALAEOENVIRONMENTS

All specimens of *Microdictyon sinicum* come from the lower part of the Yu'anshan Member, from a finely laminated mudstone deposited in a pro-delta environment. The vertical sequence including the Yu'anshan Member and its overlying Canglangpu Formation shows a coarsening-upward pattern, which has been interpreted to represent a progradational delta system. The strata of its lowest 25 m consist of organic-rich black shale and silty mudstone interpreted to represent a distal facies of the deltaic complex. The overlying 50 m consist mainly of fine clay deposits, with interbedded thin horizons of silt deposits, from a few mm to a few tens of cm thick. Bedding planes with current lineations attributed to the upper flow-regime occur abundantly within the silt beds.

The Chengjiang fauna is noteworthy not only for offering a rare glimpse of early life, but also as representing sedimentological circumstances of which we know very little. Seilacher (1991) forwarded a speculative model for the burial mode of the Chengjiang fauna, suggesting that the preservation was a result of rapid sedimentation under anoxic conditions. The sedimentary environment of the Chengjiang fauna, therefore, is an important and fascinating field. Studies have recently been carried out by a research group of Nanjing Institute of Geology & Palaeontology and a Sino-Swedish joint project (M. Lindström and Chen Junyuan).

A new restoration (Lindström and Chen in prep.) shows that the present eastern Yunnan was part of the shallow pericontinental area which bordered on the Kan-Dian land to the west. Paleomagnetic data suggest that the area belonged to the tropical Zone (Liang *et al.*, 1990). A high proportion of clay minerals in the mudstone, together with a dominant constituent of quartz in coarse-grained sediments, indicates a wet tropical climate, which might have controlled the type of sedimentation. The Lower Cambrian Chiungchussu (Qiongzhusi) Formation and its overlying Canglangpu Formation embody an upward-coarsening sequence which was formed by an eastward progradation of a delta where eject of sedimentladen water of a river or rivers intruded a body of standing water from the west (the Kan-Dian land). The entire sequence of some 150 m ranges from marine mud of distal (represented by 50 m of the Chengjiang Lagerstätte, lower Yu'anshan Member) and proximal prodelta (50 m, upper part of the Yu'anshan Member) up into the delta-front sheet sands (20-40 m of the basal Canglangpu) and fluvial sands (lower Canglangpu Formation).

The Chengjiang Lagerstätte deposition corresponds to a period of maximum water depth, when an easternward delta progradation has introduced episodically large quantities of fine material by turbidity flows into the area. The high sedimentary rate has caused the water depth to shallow upward throughout most of the time of the Yu'anshan Member deposition, with deposits reaching the sea level in the lower Canglangpu Formation. Judging from the thickness of the simple shallowing unit, the water depths of the Chengjiang Lagerstätte deposition may range from 120 m to 70 m.

Detailed sedimentary and taphonomic analyses suggest that the Chengjiang Lagerstätte was mainly formed by rapid sedimentation of localized catastrophic turbidite events of varying scale which can be classified into two basic types: 1, the rarer moderate to small scale turbidity flow represented by the sand beds, 10 to 100 cm thick, and 2, centenary microturbidite events of 1 cm fine mud beds. The mud beds contain the Chengjiang fossil fauna, and make up 90-95% of the vertical thickness of the Chengjiang Lagerstätte. Each such bed bears a lower, sharply based, graded unit and an upper fine mud unit. They presumably were micro-turbidite depositions. Grooves are the commonest sole markings found as interbed sedimentary structures. Each turbidite may have settled in a short time, ranging from a few minutes to a few hours. The thickness of the microturbidite beds suggests that the burial depth of the Chengjiang fauna was very shallow, from a few cm to ten cm in the uncompacted stage. The circumstance that the Chengjiang Lagerstätte is characterized by such shallow burial, suggests that most of the animals in the Early Cambrian had a relatively limited escape ability. A shallow rapid burial of 10 cm or less, as indicated by the Chengjiang Lagerstätte, was lethal to most of the individuals.

TERMINOLOGY

Microdictyon was bilaterally symmetrical. The median dorso-ventral plane is sagittal (abbreviation, sag.) and this plane contains the longitudinal axis. Planes parallel to, but outside, the sagittal plane are termed exsagittal (exs.). A direction away from the sagittal plane is abaxial while toward this plane is adaxial. A plane perpendicular to the sagittal plane is transverse. The ventral trunk surface is identified by the presence of legs. The body was previously considered to be tapering posteriorly, with a very short head and an elongated posterior projection. Homology analyses by Ramsköld (1992b) are confirmed by the present study and favour an anteroposterior reversal of *Microdictyon*. The prelimb-bearing portion of the body is referred to as the head. The body consistently bore nine pairs of plates along the lateral sides, instead of ten pairs as previously suggested (Chen *et al.*, 1989a). The supposed anteriormost pair present only in the holotype has proved to be a patch of stain rather than plates. The plates are referred to here in a numerical order from 1 to 9 from anterior, and abbreviated P1, P2; RP1, RP2; or LP1, LP2, etc., in the text to refer to particular pairs or to particular right (RP) or left (LP) plates. The plates differ from each other both in size and in morphology, and may be referred to four somewhat intergrading morphotypes termed here EL form (P1); R-form (P2), OV-form (P3-8) and RH-form (P9), the abbreviations standing for elongated, round, ovoid, and rhomboidal.

The different surfaces of the plates are referred to as outer or inner face, dorsal and ventral, and anterior and posterior margin. The length of the dorsoventral extent is referred to as the height (PH); the length of the anteroposterior extent is referred to as the length (PL).

The head is represented by the anterior portion of the body prior to the first pair of plates. The trunk is subdivided into nine subdivisions (sdv) which extend between the anterior margins of two successive pairs of P1-P9 except for the rear subdivision which is defined by the anterior margin of the P9 and the rear margin of the trunk. The subdivisions are referred to here in a numerical order from 1 to 9 from anterior, brevity is served by using sdv1, sdv2, etc. Each of the sdv3-sdv9 bore a round dorsal bulge in its anterior half, above the plate. The bulges are referred to here as swells. The depressed portion (relative to the swells) of the posterior half of sdv3-sdv8 is referred to simply as the depression.

The legs are numbered from anterior with abbreviations in accord with those of the plates; Lg1, Lg2, Lg3; LLg1, LLg2, LLg3; RLg1, RLg2; RLg3, etc. Leg pair Lg1 is set below plates P1, while Lg9 and Lg10 are set anterior to and behind P9, respectively.

Each specimen was divided into a part and a counterpart by the split of the rock into two slabs, each having portions adherring to it. The slab possessing the relatively more complete specimen is referred to as the part; the other slab with the less complete specimen is referred to as the counterpart.

Explanation of symbols in Text-figures

al, alimentary canal
anl, transverse annulations on trunk or legs
cc, central canal within the leg
cw, claw
dp, depressed area of the trunk
hd, head region
lg, leg
1lg (or 1l), left leg
1lg1, 1lg2, etc, left legs, numbered from the anterior
LP, left plate
LP1, LP2, etc, left plates, numbered from the anterior
m, mouth opening
p, papillae
rlg, right leg
rlg1, rlg2, etc, right legs, numbered from the anterior
RP, right plate
RP1, RP2, etc, right plates, numbered from the anterior
rpj, rear projection
P, plate
sdv, trunk subdivision
sdv1, sdv2, etc, trunk subdivisions, numbered in an ascending order from the anterior margin of the trunk sw, swell

Abbreviations in Tables

EL, entire length of an animal
L, length
△LS, amount of the length of the trunk subdivision being lost due to oblique preservation
L(1), length of left leg
SL, length of the trunk subdivision
L(w), width of left leg
OL, original length of the trunk subdivision
R(1), length of right leg
R(w), width of right leg
T°, angle of tilt
T°a, angle of tilt of the sagittal plane toward the anterior
T°d, angle of tilt of the sagittal plane toward the dorsum
T°1, angle of tilt of the sagittal plane in a longitudinal direction
T°p, angle of tilt of the sagittal plane toward the posterior
T°v, angle of tilt of the sagittal plane toward the

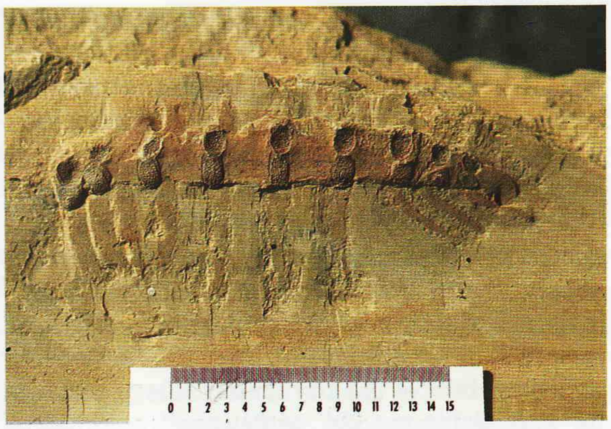
venter
TW, width of trunk
TWd, width of trunk across the depressed areas of trunk
TWp, width of trunk across the swell (at P3-P9) or plate-bearing point (at P1-P2)
PL, length of plate
PH, height of plate
VW, width of the soft-bodied ventral area which is measured as the distance between the ventral margin of the plates of a pair in a subdorsally compacted specimen.

PRESERVATION

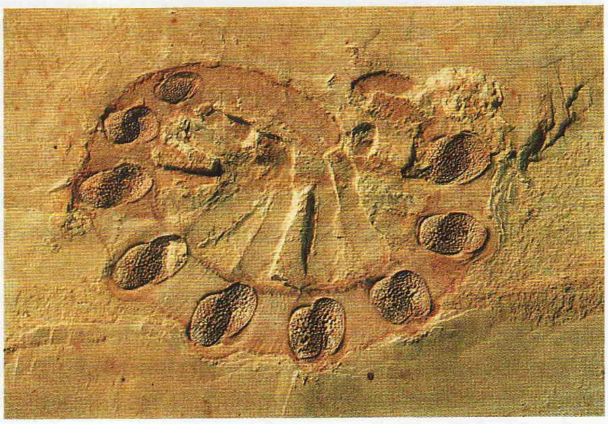
Most specimens of *Microdictyon sinicum* occur as entire individuals, although they are rarely completely uncovered through preparation. This is so because they occur in a variety of orientations with respect to the plane of bedding, including dorsally, ventrally, laterally, and a variety of intermediate orientations which are inclined dorsally, ventrally, and laterally. A curving of the longitudinal axis with respect to the plane of bedding is also recognized in a number of fossils, the longitudinal axis of which lies either at an angle to the bedding, or is folded more or less parallel to the bedding with a tendency to be inclined both posteriorly or anteriorly.

Dorsal or subdorsal compaction (Text-fig. 3), that is with the sagittal plane at right angles or nearly so to the bedding plane, has been recognized in about a dozen specimens. This is referred to here as the life position. This position was unstable during transport and subsequent settling of the surrounding sediment. The relatively common occurrence of dorsal compaction may either indicate that the animals were alive and maintained their life position while they were carried by the low density turbidity mud flow, or considering that all possible orientations except vertical are represented in the material, the dorsal compactions may be due to chance. In the cases of dorsally compacted specimens preserved on an *Eldonia,* they may be in true life position, being buried while clinging to the *Eldonia* by the claws on the legs.

Lateral specimens (Text-fig. 4), which have the sagittal plane approximately parallel to the bedding plane, are the most frequent, so presumably the anatomy favours a lateral disposition. Intermediate, oblique orientations occur commonly. In this orientation the sagittal plane lies at an angle to the bedding. The angle can be estimated from the degree of dislocation between the paired plates. More steeply inclined specimens may be referred to as subdorsally or subventrally compacted specimens.



Text-figure 3. A complete specimen (ELRC 30012) of a medium-sized *Microdictyon* which was buried in a life position, being subdorsally compacted.



Text-figure 4. A sublaterally compacted specimen (ELRC 30060) of an entire *Microdictyon* animal.

Most of the fossils appear to be twisted and curved along the longitudinal axis of the body. As an effect of compaction, both the outline and the length of all or parts of the body can be modified in different ways between areas of the body which were buried at different angles relative to the plane of bedding. The full length of the body or a certain part is represented only by a parallel preservation;

in most situations the length in the parts of the body is shorter than originally, with a varying degree of reduction which depends on the angle of burial. The relation of the angle of burial to the reducing ratio can be formulated as cos α =RL/OL(α : the angle of burial; RL: reduced length; OL: original length).

All specimens were vertically compacted during early diagenesis. When reconstructing the original shape of diagenetically flattened organisms, it is assumed that the compression resulted either in lateral expansion (Chen *et al.*, 1989a) or without having lateral expansion (Walton, 1936; Harris, 1974; Ramsköld, 1992b). New observations confirm the latter studies and show that diagenetic compaction in the laterally preserved specimens forced the parts of the body to move closer in vertical distance without horizontal dislocation of the parts or lateral expansion of the body. In the subdorsal or subventral specimens the paired plates, on the other hand, were subvertically extended before compaction. Because they were hard and could not be compacted vertically, they therefore tended to reorient into a parallel or subparallel preservation by means of rotation, which appears to have taken the lower end of the plates as pivotal points. Fossil evidence shows that the paired plates in most cases rotated unidirectionally, with a substantial lateral expansion appearing only on the active side, whereas the passive side is either contracted or unchanged, without lateral expansion. Rotation of the plates appears to have taken place at a very early stage when the cuticle of the body apparently, in several specimens, retained enough mechanical strength not to lose the attachment to the paired plates during rotation.

The maximum observed width of the compacted body has a length equal or very close to the transverse distance between the bases of the plates of a pair plus the height of the plate. This width exceeds the diameter of the body, but is shorter than the figure of $\pi \times D/2$ (D, diameter of body) describing the theoretical width yielded by a complete lateral spreading out of the cuticle.

The diameter of the body in most parts of the trunk, as indicated by parallel compactions, has a length equal to 1.25 (on depressions) to 1.6 (on swells of the trunk) times as long as the height of the associated plates. The width of depressions of ELRC 30012 is equal to 1.7 times the height of the plate. This figure is close to but slightly smaller than the theoretical figure of $\pi \times D/2$ which would give a width as much as 1.9 times the height of the plate if the cross section in the depressions of the trunk was circular.

The same situation applies to the legs which are preserved without any lateral expansion. The legs were originally divergent ventrally, and are usually preserved with one leg row parallel to and one row at an angle to the bedding plane. Varying degrees of trunk rotation and tilting result in that the length of the legs can be considerably different between the two legs of the same pair and between different pairs.

The original length of a leg can be estimated from a parallel preservation of the leg(s) which are available in a number of specimens. As indicated by laterally preserved specimens, the leg length increases anteriorly in all individuals. The preserved length, which is depending on the burial angle, however, varies among the legs, as seen in the fossils. Examination of the burial angle of the legs shows that the legs of a pair were usually diverging at approximately 90°.

The fossils are preserved within the weathered rock as a thin film either in a reddish color showing a marked contrast to the yellowish matrix or in a yellowish color close to but somewhat darker than the matrix (see Text-figs. 3 and 4) The color shows considerable variation not only among the specimens but a substantial difference is also recognizable between the various parts of the body. The traces of the alimentary canal and claws at the distal end of the legs are usually black and with a marked contrast to the surrounding soft part of the body. The central canal in the legs and the empty (as interpreted) parts of the gut are bluish gray. In well preserved specimens the color of the body appears to be darker in dorsal swells and annuli (see Text-figs. 3 and 4).

There is no definite evidence of any identifiable amount of fine mud filling within the body cavity.

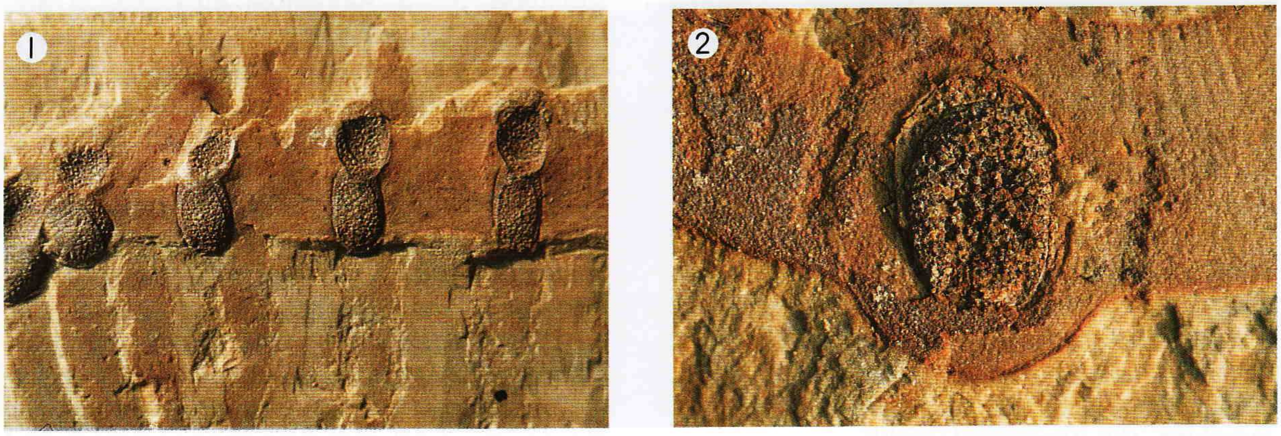
The observed varied attitudes in which the individuals of *Microdictyon sinicum* were buried include: 1, twisting anticlockwise or clockwise along the longitudinal axis; 2, curving toward the ventral side with the curvature increasing anteriorly to form a nearly circular or semi-circular course in numerous cases; 3, divergent extension of the legs; 4, either anterior or posterior curvature of the legs in Lg1-Lg9 and anterior curvature in Lg10; 5, adaxial bend of the distal portion of the legs 1-9 and a forward bend in Lg10. Some specimens show that the individuals were standing with divergent, extended legs when they were buried. In the case of individuals anchored on *Eldonia* this indicates that they were alive and therefore could maintain a life position when engulfed by the low density turbidity mud.

PLATES, THEIR GROWTH AND FUNCTION

Many Cambrian lobopodians were equipped with plates which formed a scaly of spiny armour partly covering the sides of the body, usually with a large plate lying above each of the legs. They may be flattened and deformed, without showing fractures in most forms, leading to the suggestion that in most forms the plates were made of tough, but unmineralized matter (Ramsköld, 1992b). The plates in *Microdictyon,* however, were an exception, made of very tough matter which is considered to be originally phosphatic (Bengtson *et al.,* 1986). The plates in ELRC 30041 (see pl. 10, fig. 1) appear to have been buckled without evidence of breakage, suggesting that they may have been somewhat filexible. Such plastic deformation may be explained by an incomplete mineralization of the plates.

Although the most wide-spread growth pattern for shells and many other mineralized structures is by accretion, the plates formed by this process retain all previous growth stages. Morphological comparison of the plates among the differently sized individuals reveals no trace of the presence of any early growth stages within the larger plates. The plates were thus formed in one single phase (Bengtson *et al.,* 1986). Limited data (Text-fig. 10) show the variation of length compared to height of plate. No clear moult stages, however, are indicated, suggesting that growth rate differed somewhat between individuals.

The plates were apparently formed before the individual molted, a periodically recurring phenomenon. Individuals trapped and embedded just before they were to molt may thus show both the smaller plates to be molted together with the cuticle, and the new, larger ones. Such duplicated plates (see Text-fig. 5:1) are present in a few specimens, where each duplicated pair is composed of smaller (old) plates superimposed on ones of normal (new) size (see ELRC 30012: pl. 2, figs. 1-2, pl. 3, fig. 2, Text-fig. 5:1; ELRC 30049: pl. 8, figs. 1-3; ELRC 30041: pl. 10, fig. 1; ELRC 30036: pl. 16, figs. 3-4; ELRC 30042: pl. 20, fig. 1). This



Text-figure 5. Enlargements of: 1, a portion of the trunk in ELRC 30012, showing the double plates and papillae; and 2, plates in ELRC 30008, showing a roughly hexagonal meshwork, each cell encasing a circular tube. On top of the hexagonal meshwork there are numerous small spiky projections protruding from the junctions of the walls. The spiky projections (best seen toward the ventral margin) are tapering outward rapidly to a sharp apex which tends to incline dorsally, and are preserved in a shiny black color, sharply contrasting with the underlying hexagonal meshwork which is yellowish. Remnants of a thin, reddish layer adheres to the impression of the soft tissues lateral to the plate, mainly on the right side.

duplicated occurrence is interpreted as an indication of double skins of the pre-molt stage. The linear size difference of the duplicated plates between the new larger plate and the old one ranges from 13% to 20%.

The plates formed a partial cover along the sides, each plate lying above a leg, which suggests that they may have served as a body frame and for muscle attachment (Chen *et al.*, 1989a). They were perforated by cylindrical holes. The outer surface is equipped with numerous nodes which are spiky, and mushroom-shaped. The nodes are present in all species belonging to *Microdictyon* and appear to curve dorsally (see Text-fig. 5). The function of the nodes is unknown. The tubular holes in some species are reported to be closed by a very thin hemispheric sheet on their bottom (Bengtson *et al.*, 1986; Tong, 1989). Because of this, Bengtson *et al.* believed that both closed and open tubes may abut against a basal, probably primary non-perforated apatite sheet.

TAXONOMY AND DISTRIBUTION OF PLATE-BASED TAXA

Plates of *Microdictyon* and other armoured lobopodians have a wide distribution in Cambrian rocks. The unique features of the fossil plates suggest that the plate-bearers are a closely allied monophyletic group. The oldest valid, available family-level name for this group is Eoconchariidae Hao and Shu, 1987.

Hao and Shu (1987) erected the new family Eoconchariidae for supposed primitive radiolarians including three new genera and seven species. All these taxa are based on disarticulated plates which are either identical (in *Eoconcharium* and *Fusuconcharium*) or closely allied (in *Quadratapora*) to *Microdictyon*. *Eoconcharium* and *Fusuconcharium* are thus junior subjective synonyms of the latter. *Quadratapora*, on the other hand, differs from *Microdictyon* in several respects and is considered a distinct genus (see Ramsköld 1992b for a discussion on these taxa). The family name Eoconchariidae is considered to be valid to represent *Microdictyon* and its closest allied organisms. The family was later erected a second time by Shu and Chen (1988). That family name is a homonym of the earlier erected one. Microdictyonidae Chen, Hou & Lu, 1989 is a junior subjective synomyn of Eoconchariidae Hao and Shu, 1987, and it should no longer be used.

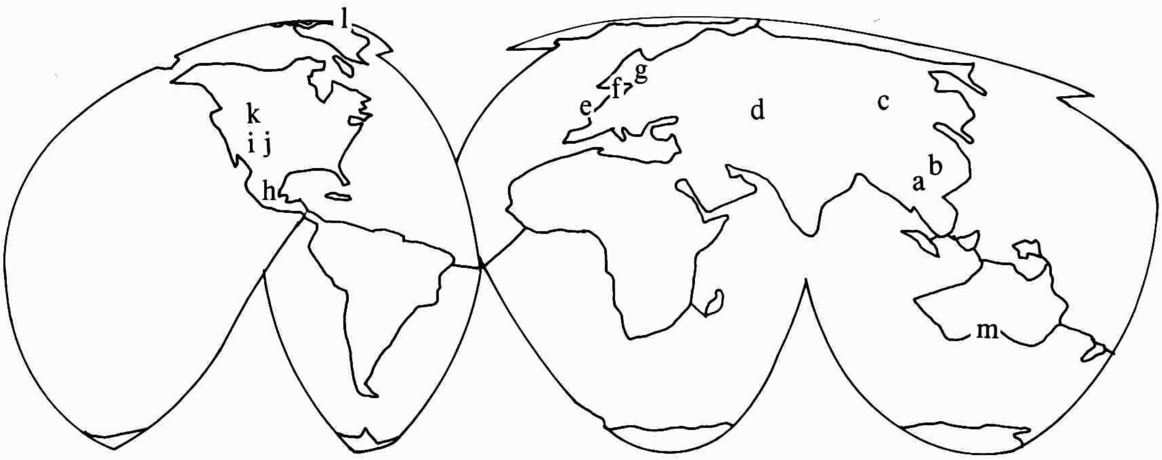
The diagnosis of the family Eoconchariidae is emended as follows: lobopodian metazoans, on the lateral sides of the body bearing paired plates which possess a hexagonal (in *Microdictyon*) or tetragonal (in *Quadratapora*) pattern of pores and nodes. At least three genera are included within this family. They are: *Microdictyon*, *Quadratapora*, and a unnamed Greenland new taxon (Text-fig. 6-1) which possessed spine-bearing plates (Bengtson, 1991). The plate-based taxa and their distribution is discussed below:

Genus *Microdictyon* Bengtson, Matthews & Missarzhevsky, 1981

(= *Fusuconcharium* Hao & Shu, 1987; *Eoconcharium* Hao & Shu, 1987; *Eoconcharium* Shu & Chen, 1988; *Fusuconcharium* Shu & Chen, 1988)

The genus was originally described from discrete plates with a hexagonal meshwork. The shape of isolated elements in *Microdictyon* has previously been used as the principal basis for a species concept by a number of authors. A new concept of multielement taxonomy in *Microdictyon* is made possible by the recently discovered complete specimens of *Microdictyon sinicum* which display nine pairs of lateral plates. These display a range of morphologies, divided into the four types defined here as: EL (elongated); R (round): OV (ovoid) and RH (rhomboidal). For description and comparative purposes, the plates are here oriented in the same manner as on the host animal. That is, the dorsal margin is up and the anterior margin facing anteriorly on the body. The concave side attaches to the body whereas the convex side is facing away from the body. The identification of the dorsal and ventral sides presents no problem for most of the discrete plates, and is facilitated by the ovoid outline of OV forms which face dorsally with the narrower side. The small surface spines which are seen in *M. sinicum* and in the isolated plates of the OV form belonging to other *Microdictyon* species, are inclined upward (dorsally) without exception. They occur in all plates, and therefore provide unequivocal evidence for reconstructing of the original orientation of the isolated plates.

The plates of *Microdictyon* had a potential for fossilization in normal environments, and show a broad distribution in Lower and Middle Cambrian rocks (Text-fig. 6). A number of species have been



Text-figure 6. World map showing the localities yielding *Microdictyon* and its closely related taxa. a), Chengjiang, E. Yunnan; China (L Cambrian); b), Zhenba, S. Shaanxi, China (L Cambrian); c), Siberia, Russia (L Cambrian); d), Kazakhstan (L Cambrian); e), Shropshire, England (L Cambrian); f), Denmark (L Cambrian); g), Sweden (L Cambrian); h), Mexico (L Cambrian); i), Nevada, USA (L Cambrian); j), Utah, USA (M Cambrian); k), British Columbia, Canada (L Cambrian); 1), Greenland (L Cambrian); m), S. Australia (L Cambrian).

described since 1981 on the basis of the shape of the discrete plates. They show the following morphological variations among the different species: 1, outline of the plates; 2, shape of the spines; and 3, size of the tubes. We have compared the ratio of height against width in the plates of different individuals of *Microdictyon sinicum.* Each element has a certain proportion between the height and width. The spines vary greatly among the species, in shape ranging from mushroom-like or short to an elongated conical form. The tubes show a certain range of variation in each species and can be different between the species. The discovery of completely preserved *Microdictyon* animals makes it possible to define the taxonomic units on the basis of the natural assemblage of the plates. Each of the taxa named until now are discussed below:

Microdictyon effusum Bengtson, Matthews and Missarzhevsky, 1981 is a single element form based on OV-form plates collected from the Lower Cambrian Geress Member of the basal Shabakty Formation (upper Atdabanian), Malyj Karatau, Kazakhstan (Text-fig. 6-d). The OV-form is 1.92 mm in height, twice as long as the width which measures 0.9 mm; tubes range from 0.13 mm to 0.01 mm at girdle; spines short, mushroom-shaped with pointed, conical tip, having a diameter of 0.05 mm at base and a vertical extension of 0.04 mm, with apex inclined dorsally. The species differs readily from *Microdictyon sinicum* by having its OV-form of plates much narrower, and the tubes are smaller.

Microdictyon rhomboidale Bengtson, Matthews and Missarzhevsky, 1986 is a single form species. All the plates illustrated are of RH-form, from the Lower Cambrian (upper Atdabanian), Kazakhstan (Text-fig. 6-d). This RH-form shows a complicated margin with a well defined, presumably anterior angular extension and a concave ventral side, having a width considerably longer than the height, measuring; 1.1 mm and 0.67 mm in holotype; tubes small in diameter, ranging from 0.04 mm to 0.01 mm; spines mushroom-shaped, with rounded or hat-shaped tip. This species can be readily distinguished from *Microdictyon sinicum* by its complicated shape of the RH-form plates, the smaller tubes and mushroom shaped spines. It differs from *M. effusum* by having differently shaped spines and smaller tubes. (The orientation of *M. rhomboidale* is slightly uncertain. Judging from the direction of the spines, the plates could be directed with the long axis vertically, not longitudinally. However, if they are oriented longitudinally, they are of a shape similar to P1 in *M. sinicum,* not P9, i.e., not RH shape but EL).

The plates referred to as *M.* cf. *rhomboidale* by Bengtson *et al.,* 1986 from the Lower Cambrian Sekwi Formation (corresponding to the lower part of *Nevadella* Zone), Mackenzie Mountains, British Columbia, Canada (Text-fig. 6-k), belong respectively to the RH and OV form. The plates of RH-form are polygonally outlined and modified ventrally with a deep concavity and two distinctive projections. A well defined angular extension is present both anteriorly and posteriorly. Tubes ranging from 0.08 mm to 0.01 mm. The plate in OV-form is narrowly egg-shaped. Spines are mushroom-shaped with low, conical tip, inclined dorsally, measuring 0.06 mm at the base and being 0.04 mm tall. The plates are considered here to represent a new species which differs from the closely related species *M. rhomboidale* by having a more complicated outline of the plates of RH-form and the short, conical shape of the spines.

M. robisoni Bengtson, Matthews and Missarzhevsky, 1986 from the Middle Cambrian Swasey Limestone (corresponding to *Ptychagnostus gibbus* Z. or its immediate underlying strata), Utah, USA (Text-fig. 6-j), is represented by plates belonging to the RH and OV forms. The plate in RH form (their Fig. 8-A), is incomplete, 1.4 mm in width and with an estimated height of 1 mm; with tubes ranging from 0.08 mm to 0.01 mm. The plate in OV form (their Fig. 9-A, B, C) is subcircular, 0.43 mm wide and 0.53 mm high, with tubes ranging from 0.025 mm to 0.01 mm. The other plate in the same form (their Fig. 9-G, H) is 0.44 mm times 0.57 mm.

All the plates referred to *Microdictyon* sp. 1 in Fig. 10 of Bengtson *et al.* (1986), from the Lower Cambrian Campito Formation (lower part of *Nevadella* Zone), Nevada, USA (Text-fig. 6-i), are fragmentary and possibly belonging to the EL form (their Fig. 10-F) and OV-form (their Fig. 10-A). The plate in EL-form is 1.5 mm wide and 0.9 mm long, with tubes ranging from 0.04 mm to 0.11 mm. The plate of OV-form has tubes in the same range as the EL form. The spines are short, mushroom-shaped with hat-shaped tip.

The plates illustrated as *M.* spp. in Fig. 12 by Bengtson *et al.* (1986) represent two species. One is from the Kalby Marl, Bornholm, Denmark (Text-fig. 6-f), and is represented by two plates of OV-form. The larger one is 2.3 mm high and 1.6 mm wide, with tubes in a diameter of 0.12 mm. The other one is from "Fragment Limestone", Scania, Sweden (Text-fig. 6-g). These plates are fragmentary, but represent a distinctive species with plates which bear mushroom-shaped spines, each having an elongated 'stem'.

M. sphaeroides Hinz, 1987 from the Lower Cambrian Tommotian stage, Shropshire, England (Text-fig. 6-e), is represented by plates of OV-form. The holotype (Hinz 1987, pl. 1-8) is in OV-form, 1 mm high and 0.83 mm wide; tubes ranging from 0.1 mm to 0.06 mm; spines coniform, having a diameter of 0.1 mm at the expanded base and a vertical extension of 0.15 mm, with a sharp apex inclined dorsally. The species differs from *M. sinicum* by having subcircular plates of OV-form, and in smaller tubes and longer spines.

M. depressum Bengtson *in* Bengtson *et al.,* 1990 comes from the Lower Cambrian Ajax Limestone, South Australia (Text-fig. 6-m). The type specimens belong to the OV-form. The holotype is 1.8 mm high and 1.07 mm wide, with tubes ranging from 0.12 mm to 0.05 mm; the plate shown in Fig. 212-A, 0.69 mm wide and 0.85 mm high, with tubes ranging from 0.07 mm to 0.04 mm; plate in Fig. 212-C being 0.48 mm wide and 0.57 mm high. Spines are low, mushroom-shaped, with a broadly conical top face with the apex situated slightly dorsal to center.

Microdictyon chinense (Hao & Shu, 1987) (= *Eochoncharium rhomboidale* Hao & Shu, 1987; *E. ovalum* Hao & Shu, 1987; *E. chinense* Shu & Chen 1988; *Microdictyon anus* Tong, 1989) comes from the Lower Cambrian Shuijingtuo Formation, Zhenba, Shaanxi province (Text-fig. 6-b). As pointed out by Ramsköld (1992b), the plates are identical to *Microdictyon* in morphology and *Eoconcharium* is thus a junior subjective synonym of *Microdictyon*. Ramsköld (1992b), as first reviser in the sense of the ICZN, chose *E. chinense* as senior synonym of the simultaneously published *E. ovalum* and *E. rhomboidale,* and discussed the homonymy of the latter species with *M. rhomboidale* Bengtson, Matthews & Missarzhevsky, 1986. To the synonyms of *M. chinense* we here add *Microdictyon anus* Tong, 1989, also from the Lower Cambrian Shuijingtuo Formation, Zhenba, Shaanxi province. Ramsköld (1992b) further discussed the homonymy of *Eoconcharium* Shu & Chen, 1988 with *Eoconcharium* Hao & Shu, 1987, and by his lectotype selection, among the syntypes of *E. chinense* Shu & Chen, 1988, of the specimen earlier designated as the holotype of *E. chinense* Hao & Shu, 1987, the former species became an objective synonym of the latter, and can therefore no longer be used. *M. spiniferum* (Hao & Shu, 1987) differs from *M. chinense* in the shape of the spines, and we follow Ramsköld (1992b), in tentatively regarding it as a separate species. *M. chinense* (Hao & Shu, 1987) is represented by several isolated plates belonging to the EL form (Tong 1989, pl. 1, fig. 3), R-form (Tong 1989, pl. 1, fig. 5), OV-form (Tong 1989, pl. 1, figs. 1, 2, 4, 8) and RH-form (Tong 1989, pl. 1, fig. 7). Tubes ranging from 0.13 mm to 0.01 mm, having a round concave bottom. Spines short, mushroom-shaped with hat-shaped tip.

Quadratapora Hao and Shu, 1987

Type species Quadratapora zhenbaensis Hao & Shu, 1987

The plates of *Quadratapora* show distinct, apparently homologous similarities to representatives of *Microdictyon* and were formed by an organism closely related to *Microdictyon*. *Quadratapora* can be readily distinguished from *Microdictyon* by the dense, tetragonal rather than hexagonal pattern of nodes and the considerably smaller tubes. Only two species are known, both of Lower Cambrian age, from China (Text-fig. 6-b) and Siberia (Text-fig. 6-c), respectively.

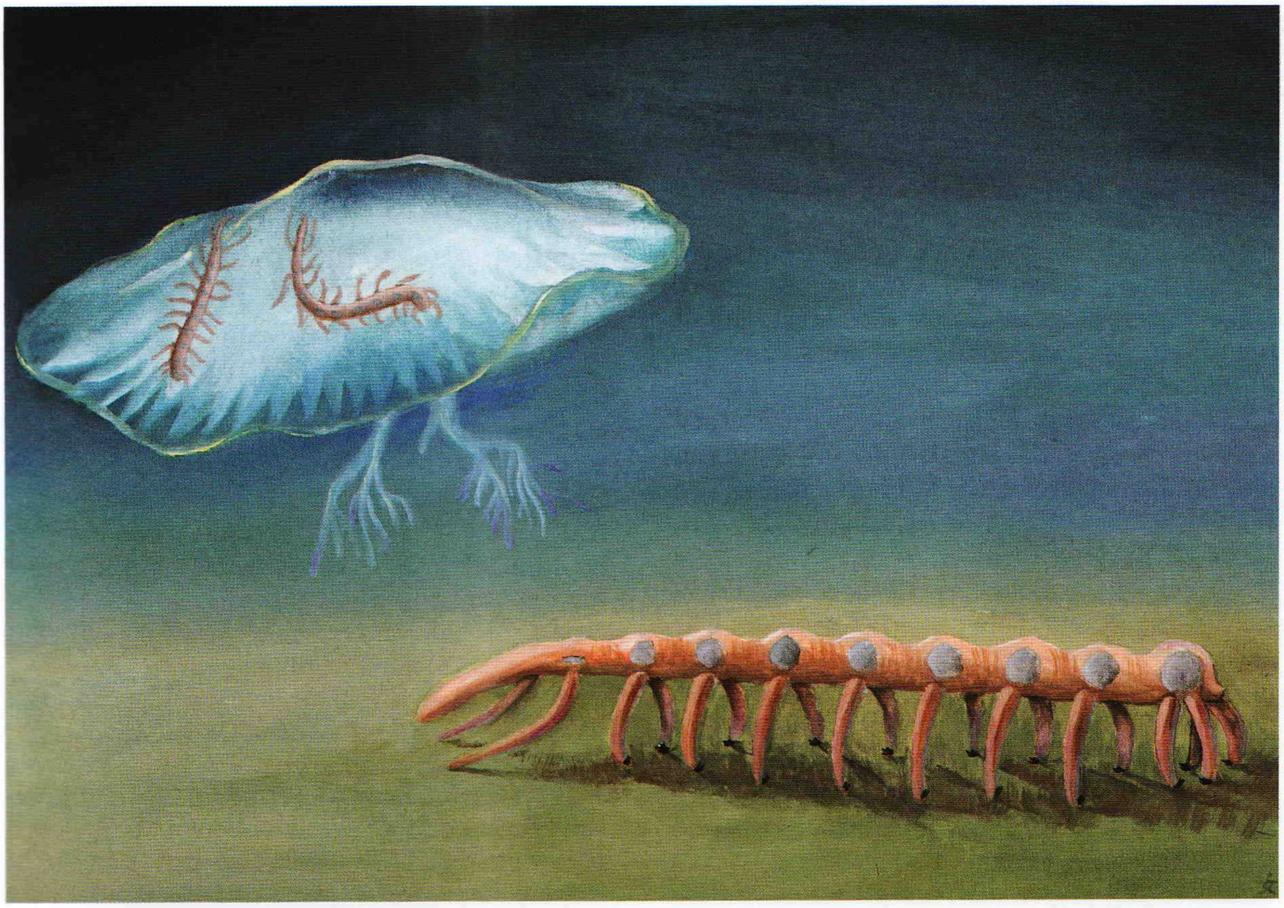
Q. zhenbaensis Hao & Shu, 1987. The single plate is of RH-form and came from the Lower Cambrian Shuijingtuo Formation, Zhenba, Shaanxi province, China (Text-fig. 6-b). The holotype (Hao & Shu, 1987, pl. 4, fig. 4) has a diameter of 0.7 mm, with small and tetragonal disposition of pores which measure 20 μm. The nodes are tetragonally arranged and mushroom-shaped.

M. teniporatum Bengtson, Matthews and Missarzhevsky, 1986, is here assigned to *Quadratapora* Hao and Shu, 1987. The single known plate is of R-form (their Fig. 11) and cames from the Lower Cambrian Tommotian stage, River Lena, Siberia (Text-fig. 6-c). The holotype has a diameter of 1.4 mm, with tubes averaging 0.02 mm; all spines show a flattened distal front, similar to in the type species *Quadratapora zhenbaensis* Hao and Shu, 1987.

MODE OF LIFE

Microdictyon appears to have been epibenthic and to have moved about by means of its legs and perhaps the longitudinal extension and contraction of the body (Text-fig. 7). The body and legs were both soft-bodied, having a high flexibility. The fossil evidence shows that the body was annulated, with an accordion-like surface permitting a ventral curvature. Several specimens show that the flexibility was much higher in the anterior portion which was able to bend into a subcircular shape (see pl. 6, fig. 2; pl. 7, figs. 1-2; pl. 10, fig. 2; pl. 11, fig. 1). Most specimens of *Microdictyon sinicum* are preserved in a curved or coiled manner placing the venter on the concave trunk side with exception of one specimen which shows a gentle curvature in a dorsal direction (ELRC 30005; pl. 20, fig. 2). Such coiled preservation, usually with the venter on the concave side, was observed by Dean *et al.* (1964) in modern annelids and arthropods that died of anoxic suffocation. A number of fossil, worm-shaped groups both from the Burgess Shale (for example *Aysheaia*) and Chengjiang Lagerstätten also show such curved or coiled preservation. Such preservation in *Microdictyon sinicum* suggests that the animal coiled up before dying from suffocation.

The legs bore terminal claws with their tips facing against the corresponding leg of the opposing row, except for the posteriormost claws which appear to point anteriorly with their tips. The claws were not very useful for walking on the muddy substrate but would have aided in climbing and holding on (Whittington, 1978). The anteriorly facing claws in the posteriormost legs would serve as anchorage to hold the posterior portion of the body on a floating or elevated object while the anterior part was freely extended, searching for new ground, much the same as insect larvae do. In modern bombycid larvae (a common kind of butterfly), two or three posterior leg pairs suffice to anchor the long body in its search for a new holdfast. In the fossil *Microdictyon* material the legs diverged at right angles and were apparently flexible, with an ability to modify themselves into an arc or a sharply bent form with the concave side facing anteriorly. Legs that are usually diverging ventro-laterally and could shape themselves into an anterior-directed curvature, are apparently useful both for climbing and for holding on to suitable substrates. It may be noted that Recent



Text-figure 7. Restoration of the *Microdictyon* animal, which is interpreted to be an epibiontic form living on the surface of the sediment, moving by means of its legs and perhaps the longitudinal extension and contraction of the body. Instead of a benthic mode of life, many juvenile or medium-sized *Microdictyon* were adapted to a pseudopelagic life style on a floating body, *Eldonia*. The *Eldonia* animal was a major faunal component in the Cambrian, with a medusiform body shape and a pelagic life style.

onychophorans have retractable claws and usually walk on their walking pads while switching to the claws only on slippery or soft substrates (Ruhberg, 1985).

Although sponges are common in the Chengjiang fauna, *Microdictyon* specimens rarely occur on the same slab of rock as a sponge. They are, however, associated with *Eldonia* to an exceptional degree. Of the 67 specimens (including 10 specimens illustrated by Chen *et al.*, 1989a) known to us up to 1993, at least 13 *Microdictyon* individuals occur in direct contact with *Eldonia* and the others are mostly present in the same turbidite mud layer in which *Eldonia* mass-occurs. Table 1 shows that the 13 *Microdictyon* were usually attaching one at a time to a floating object (pl. 1, fig. 2 and pl. 14, fig. 1), except for one slab that shows at least seven *Microdictyon* attached to a single *Eldonia* (see pl. 3, fig. 1; pl. 4, fig. 1). In addition to the seven *Microdictyon,* there is one *Cardiodictyon* and five inarticulate brachiopods belonging to *Lingulella chengjiangensis* (Jin *et al.*, 1993) which are present in a direct contact with the same floating object (pl. 3, fig. 2; pl. 4, fig. 1 and Text-figs. 13 and 14). Most of the *Microdictyon* which co-occur with *Eldonia* were buried in life position, that is, they are approximately dorsally compacted. The large size of the *Microdictyon* sample confirms the close interactions of *Microdictyon* with *Eldonia,* indicated both by their co-occurrence within the same mud bed (see pl. 5, fig. 2) and by the circumstance that juveniles of *Microdictyon* are usually preserved in a direct attachment to *Eldonia*. This strongly indicates that *Microdictyon* was commonly living in a pseudopelagic life style on a floating body, the *Eldonia* animal (Text-fig. 7). This fact should be taken into consideration when the distribution of the various *Microdictyon* species are discussed.

Eldonia was a major faunal component in the Cambrian, showing a medusiform body plan and a pelagic life style. The animal was soft-bodied and low bell-shaped, 60 mm to 100 mm in diameter. The floating body of *Eldonia,* as seen in our collections, shows a direct association with *Microdictyon, Paucipodia* nomen nudum (Chen *et al.,* 1995), *Cardiodictyon* and inarticulate brachiopods. The coexistence of pelagic *Eldonia* with sessile organisms and benthos suggests that *Eldonia* was a floating support for these pseudopelagic organisms which attached themselves with their pedicle (in the case of inarticulate brachiopods) or with clawed legs (*Microdictyon, Paucipodia* and *Cardiodictyon*).

ELRC 30046 (see pl. 14, fig. 1) represents a specimen of a relatively small *Microdictyon* with an original length estimated to have been about 21 mm. It was attaching to the top surface of an *Eldonia* which was buried up-side down.

In rare cases, as shown by the fossil evidence (pl. 3, fig. 1 and pl. 4, fig. 1), a single *Eldonia* (about 70 mm across) could support more than seven individuals of *Microdictyon*. They range in size from 11mm to 39 mm (Table 1).

Based on the available, scant evidence, we assume that the terminal mouth was small, surrounded by a circular soft lip, and without jaws. There is no evidence of eyes. All circumstances suggest that *Microdictyon* was microphagous, feeding on nutrient particles either on the surface of the sediment or host organism, or, less likely, in suspension in the water while they were floating, or on the surface of the sediment. The alimentary canal is preserved in a dark colour, almost always without showing a recognizable mud filling. This suggests that the animal was not a deposit feeder which collected the organic matter by swallowing large quantities of mud.

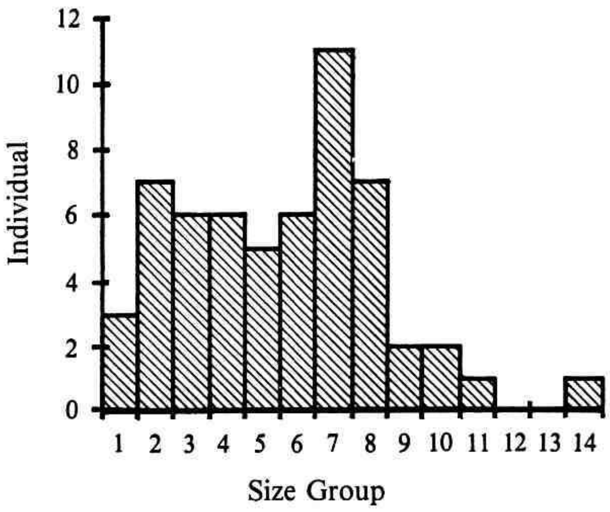
Table 1. Estimated complete, extended length and orientation of *Microdictyon* specimens hosted on *Eldonia*

Specimen no.	entire length	orientation
NIGP108294	17 mm	subdorsal
NIGP108295	17 mm	subdorsal
NIGP108296	13 mm	subdorsal
ELRC30013	10 mm	sublateral
ELRC30018	40 mm	oblique
ELRC30033	22 mm	subdorsal
ERLC30045	23 mm	subdorsal
ERLC30046	21 mm	subdorsal
ELRC30062	17 mm	subdorsal
ELRC30063	27 mm	subdorsal
ELRC30064	39 mm	oblique
ELRC30065	20 mm	subdorsal

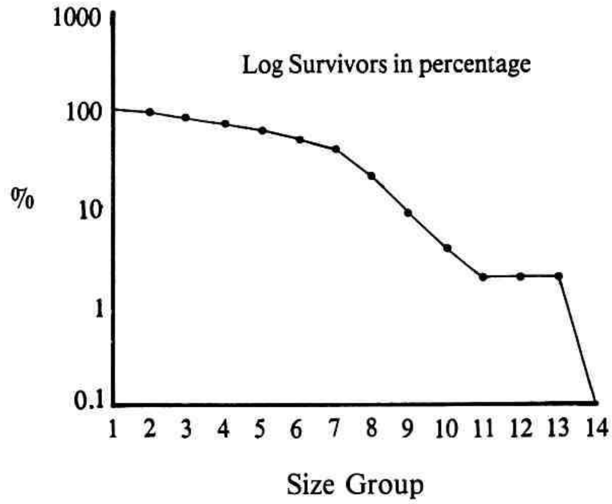
SIZE FREQUENCY

Because the longitudinal axis of the body was twisted or curved, with different body parts occurring either in parallel preservation or at varying angles to the plane of bedding, both the trunk and the legs have a preserved length which ranges from close to the original to considerably modified (shortened). Their original length cannot therefore, in most cases, be measured directly from the fossil. Fortunately, there are some specimens showing parallel preservation of the major part of body, thereby providing data on the original length both of the entire body and its parts. In most specimens, the parallel preservation is available in one or several parts of the body. The relative proportions of the parts compared with the entire length of the animal as shown by the fossil, is relatively constant among the individuals. The original length of the entire animal in most of the incompletely preserved specimens can be restored with a relatively good confidence.

The original length in 57 specimens of *Microdictyon sinicum* has been calculated, yielding a size range of 11 mm to 76.7 mm with 14 size groups classified by an increment unit of 5 mm. Most of the specimens measured are preserved within a turbidite mud layer associated with mass occurrence of *Eldonia*. The fossil assemblage of *Microdictyon* was thus probably killed by sudden



Text-figure 8. Size-frequency histogram of *Microdictyon sinicum;* size groups 1-14 which correspond to a size ranging from 10mm to 80mm; each group ranging a size of 5mm.



Text-figure 9. Size-survivorship curve of *Microdictyon sinicum;* size groups 1-14 ranging a size from 10mm to 80mm; each ranging a size of 5mm.

sedimentary event(s), presenting census population(s). The size-frequency histogram (Text-fig. 8) shows that the mortality was high in juveniles (in a size less than 10 mm), and low in adult (including the size groups 2 to 8; corresponding to a size range of 15 mm-50 mm), then increasing again at a late stage from a size larger than 50 mm. The upper range of the size in this species is recorded at 76.7mm in the holotype. The survivorship in this species (Text-fig. 9) shows a weakly convex mode suggesting that *Microdictyon sinicum* had a good immunity against mortality during most of the life time.

AFFINITIES

Microdictyon animals were soft-bodied, and they would usually be destroyed soon after their deposition on the sea bottom or in a sedimentary layer. The fossil record of these animals is, therefore, meager, and they are either absent entirely or represented only by isolated plates. The fossil plates show a wide distribution of the animal in the Cambrian marine environment, but provide limited clues to the nature and affinity of their bearers (Bengtson *et al.*, 1986). Fortunately, the complete *Microdictyon* specimens from the Chengjiang Lagerstätte show superb soft-bodied preservation (Chen *et. al.*, 1989a). These authors originally described *Microdictyon* as a problematicum, but Ramsköld and Hou (1991) drew attention to the similarity between it and extant Onychophora. In his recent papers, Ramsköld (1992a, b) demonstrated a strong similarity among Cambrian lobopodians including *Aysheaia, Xenusion, Luolishania, Microdictyon, Hallucigenia, Onychodictyon* and *Cardiodictyon.* The conventional dorsoventral orientation of *Hallucigenia sparsa* introduced by Conway Morris (1997) was shown to be in error by Ramsköld and Hou (1991). Also the anteroposterior orientation was questioned by Ramsköld (1992a), and the evidence was presented by Ramsköld (1992b). *Hallucigenia sparsa* was accordingly reversed both anteroposteriorly and dorsoventrally. The recent discovery in the Chengjiang fauna of a new species of *Hallucigenia* (Chen *et al.*, in prep.) has provided evidence for further refinement of the reconstruction given by Ramsköld (1992a). In the new reconstruction, *Hallucigenia sparsa* has an elongated body bearing seven pairs of slender lobopod limbs based ventrolaterally, each below a trunk plate carrying a long, sharp spine, plus an additional pair of rear limbs and two pairs of narrower and longer limbs that are based ventrolaterally on the neck-like portion of the head region. The head is elongated, with no significant morphological difference from the trunk. The body continued largely unchanged posteriorly behind the posteriormost pair of limbs, forming a short, weakly tapering rear extension.

Inference from postulated homologies between *Hallucigenia* and *Microdictyon* leb to an anteroposterior reversal also of *Microdictyon* (Ramsköld 1992a, b). In the new reconstruction, *Microdictyon* has an elongated body bearing 10 pairs of lobopod limbs, one beneath each plate pair plus a posterior pair. The head was elongated, without a significant morphological difference from the remainder of the body.

In a homology analysis of the Cambrian lobopodians, Ramsköld (1992b) gave comprehensive evidence, based on 12 characters, for the status of the group as monophyletic. The present study of the morphology of *Microdictyon* confirms his observations and interpretations for *Microdictyon* in his characters 1-6 and 8-12. For character 7, he stated that the evidence for annulation in the trunk of *Microdictyon* was weak. New material shows distinct, sharply crested annulation in the trunk (and the legs) of several specimens. This and other new knowledge provides evidence to strengthen the close ties among the Cambrian lobopodian worms, as indicated by their important, uniquely shared features. Apart from the 12 characters discussed in detail by Ramsköld (1992b), they all possess a cylindrical, soft-bodied, worm-like body. The paired limbs which extend ventrolaterally from the body are of lobopod type. Each trunk plate is lying above a limb. The head is indistinctly defined from the body, and it has a terminal mouth. The rear extension, which occasionally is lacking, is interpreted as an anal extension. There is no evidence of jaws or eyes; the structure in the head of *Onychodictyon* reported by Ramsköld (1992b, fig. 4) as a possible jaw is now known from better preserved material to be a strongly sclerotized shield covering the head, and the paired structures anteriorly in one *Microdictyon* specimen tentatively regarded by him as jaws have not been observed in more specimens.

Diversification of Cambrian lobopodians had already started in the sea far back into the early stages of what is known as the "Cambrian Explosion", as is shown by many aspects of external morphology, for example the variation in the number of leg pairs, ranging from 7 to more than 23. The body in a number of forms (*Microdictyon, Hallucigenia, Luolishania, Xenusion,* and *Cardiodictyon*) has an anal projection behind the last pair of legs whereas the body in *Aysheaia* and *Onychodictyon* teminated at a pair of legs. Anterior, modified limbs are present in the head region at least in *Aysheaia* and *Hallucigenia,* but of very different types. The sides are armoured with plates which vary in morphology among the different forms, from tubercles in *Luolishania* and *Aysheaia,* spiky form in *Hallucigenia,* convex plates with a distally extended spines in *Xenusion* and *Onychodictyon,* reticulated plates in *Microdictyon* and *Quadratapora,* and subtriangular plates in *Cardiodictyon.* The plates in most forms were of tough organic, but possibly unmineralized matter while they appear to have been substantially mineralized in *Microdictyon* and *Quadratapora.*

The monophyly of the Cambrian lobopodians appears to be secure. The wider phylogenic position however, is still unclear. The morphological similarities have led a number of authors to regard the Cambrian lobopodians as members of the Onychophora (Walcott, 1931) or of a widened onychophoran concept (Ramsköld and Hou, 1991; Ramsköld, 1992a, b). Hutchinson (1930) assigned the Burgess Shale lobopodian *Aysheaia* to a separate extinct order of the Onychophora. Delle Cave and Simonetta (1975) and Simonetta (1976), however, drew attention to similarities also with the Tardigrada, suggesting that *Aysheaia* was intermediate between Tardigrada and Onychophora. Whittington (1978), on the other hand, considered it as a problematicum. Later also *Xenusion* was considered to bear similarities with Recent Tardigrada (Dzik and Krumbiegel, 1989).

To evaluate the wider phylogenetic position of the Cambrian lobopodians, we must examine the position of the Onychophora and the fate on the now dismembered phylum Uniramia. The Uniramia was informally conceived Tiegs by (1947) to embrace the Hexapoda (insects and related groups), Myriapoda (millipedes and centipedes), and Onychophora (the velvet worms). The group was further refined by Tiegs and Manton (1958) before Manton (1972) formally erected the Uniramia. According to Manton, all these groups are characterized by two main features; firstly, the uniramous legs, and secondly, the development of the mandibles from a whole leg; the latter feature was thought by Manton (1972, 1977) to be the main evidence for the groups' close affinity. However, the division between uniramous and biramous forms has recently been repeatedly proven to be artificial. On the basis of observations on Lower Permian insects, supported by data from recent taxa, Kukalová-Peck (1992) suggested that the uniramous and biramous conditions are both secondarily derived from a polyramous condition. The other 'shared' character, the 'whole leg' origin of the mandibles has also been questioned (Kukalová-Peck, 1991), and the idea was forwarded that hexapods, myriapods, chelicerates, and crustaceans have jaws identically composed of the five elements of an arthropod coxapodite (if so a character constituting an important synapomorphy for these Arthropoda). In onychophorans, on the other hand, the jaws indeed show a 'whole leg' origin. Other lines of evidence carry perhaps more weight in splitting the unity of the 'Uniramia'. Molecular analyses of 12S ribosomal RNA sequences indicate that onychophorans are closely related to arthropods. A study based on restricted data (Ballard *et al.*, 1992) indicated ingroup arthropod status of Onychophora, with the Myriapoda as sister group of all other arthropods. The results were, however, weakly supported, and in a re-analysis of the original data, Fortey and Thomas (1993) found that "the base changes supporting the phylogeny, in particular the placement of the myriapods, are few in number and questionably robust". Indeed, when fossil taxa are added to the proposed phylogeny curious results emanate (Budd, 1993), such as independent arthropodization of myriapods and other arthropods. Better supported results were recently published by Wheeler *at al.* (1993) in a comprehensive study of arthropod phylogeny based both on molecular evidence and morphological data. Wheeler *et al.* (1993) found strong evidence for a monophyletic Arthropoda including Onychophora as the sister group of all other arthropods. Both molecular data sets used (18S rDNA and ubiquitin) disproved monophyly of 'Uniramia', as did the morphological analysis based on 100 characters. They found the Tracheates (Myriapoda + Hexapoda) strongly supported, and stated: "The union of Onychophora with Tracheates is overwhelmingly refuted".

Among other groups that from time to time have been included in the 'Uniramia' is the Pentastomida (the parasitic tongue worms), a group also commonly regarded as a separate phylum. An early study by Wingstrand (1972) on spermatozoan morphology suggested crustacean affinites, but this idea was largely ignored until recently when Abele *et al.* (1989) presented molecular evidence from 18S ribosomal RNA sequences which supported Wingstrand's results. Well preserved, primitive pentastomids from the Upper Cambrian show arthropod affinity, but rather than being modified crustaceans, pentastomids may have branched off before the euarthropod level (Walossek and Müller, 1994). The position of other groups often allied with or included in the 'Uniramia', such as the Tardigrada, is less certain. No molecular data on the Tardigrada have yet been published, and Wheeler *et al.* (1993) left their position unresolved.

The above studies have a certain bearing on the phylogenetic position of the Cambrian lobopodians. With no 'Uniramia' umbrella to shelter them, a search for homologus structures shared between the Cambrian lobopodians and some well defined group must be carried out in order to define their affinities. Since molecular methods cannot be used in the fossil material, only comparative anatomy is available. Comparisons between *Aysheaia* and onychophorans were made at an early stage (Resser in Walcott, 1931), and later also *Xenusion* was regarded as ancestral both to Recent Onychophora and Tardigrada (Dzik and Krumbiegel, 1989). These two taxa were together with *Hallucigenia* and three Chengjiang forms allied with the Onychophora by Ramsköld and Hou (1991), and ingroup homology analyses indicated the monophyly of this Cambrian group (Ramsköld, 1992b). The latter author's grouping of the Cambrian taxa with the Recent Onychophora has been accepted (e.g. Bengtson 1991; Gee, 1992; Gould, 1992; Levinton, 1992; Shear, 1992; Conway Morris, 1993; Fortey and Thomas, 1993; Ghiselin, 1993). The exact nature of the relationship is, however, less clear. Features such as the paired trunk plates may indicate that most or all of the Cambrian forms constitute a separate line with close relationship with the Recent onychophorans (Ramsköld and Hou, 1991), either as a single sister group or as a basal sequence of stem taxa. An attempt at a phylogenetic analysis will be presented elsewhere (Ramsköld and Chen, in prep.). At present we leave the relationships between Cambrian lobopodians and Recent onychophorans as unresolved. Both groups do, however, unquestionably belong to the Arthropoda.

MORPHOLOGY OF *MICRODICTYON SINICUM*

The dorsoventral orientation of *Microdictyon sinicum* is regarded here as well founded because without any question its paired legs are placed on the ventral side (Chen, Hou and Lu, 1989). In their paper, this animal was restored as having an anteriorly expanded trunk and elongated tail, since the body in most of the known animals is expanded in one direction. In the accompanying restoration, the *Microdictyon* animal bore a long tail while the head region was very short or almost absent. The anteroposterior orientation was reversed by Ramsköld (1992b), and the present evidence confirms the reversion.

In the new restoration (Text-fig. 7), *Microdictyon sinicum* was a bilaterally symmetrical non-mineralized metazoan, and armoured with nine pairs of plates along its sides. The body was cylindrical between the first and last pairs of plates. The extension anterior to the first pair of plates is interpreted as the head, which is not distinctly different from the remainder of the body. As shown in a number of specimens, the head was circular in section, narrowly elongated and weakly conical, decreasing gradually in diameter anteriorly, with a rounded front (pl. 3, fig. 2; pl. 6, fig. 2; pl. 7, figs. 1-2; pl. 8, fig. 1; pl. 10, fig. 2; pl. 11, fig. 1; pl. 13, fig. 2). A structure interpreted as the mouth is expressed by a small dark spot (about 0.1 mm in diameter) lying subcentrally at or near the front margin of the head (ELRC 30011, pl. 11, fig. 1; and ELRC 30017, pl. 17, fig. 1). The spot appears to be connected with the alimentary canal (see ELRC 30012, pl. 3, fig. 2; ELRC 30049, pl. 8, fig. 1; ELRC 30017, pl. 11, fig. 1). The external surface of the head lacks visible traces of annuli, and appears to be smooth originally. The head was flexible and is usually preserved with a ventral, sometimes subcircular curvature, but is occasionally held straight, implying that the head could modify its shape considerably. The head ranges from 5.6 mm to 17 mm in length, having a maximal width ranging from 1.3 mm to 2.6 mm, corresponding to 15% to 25% of the length of the entire animal (see Table 2).

The body bore 10 pairs of unjointed legs, each of pairs Lg1-8 situated ventrally to the plates except for Lg9-10 which lie respectively ventro-anteriorly and ventro-posteriorly to the ventral curvature of P9. The width of the body is about 1/20 of the extended length of the entire animal.

Table 2. Original, extended length of head (HL) and entire animal (EL), and length of the head relative to the entire length of animal (HL/EL), expressed in percent

Specimen no.	HL(mm)	EL(mm)	HL/EL
ELRC30007	5.6	38	15%
ELRC30008	10.9	53.7	20%
ELRC30011	12	50	24%
ELRC30017	7	40	18%
ELRC30060	6.6	39.3	17%
ELRC30061	6.8	38.7	18%
NIGP108286	16	76.7	21%
NIGP108287	11	44.5	25%

The trunk is subcylindrical, except for its anterior two segments which expand in width posteriorly. It can be subdivided longitudinally into 9 subdivisions (abbreviated: sdv) by the 9 pairs of plates (measured between their anterior margins) except for the posterior one which lies between the anterior margin of P9 and the rear end of the trunk (see pl. 1, fig. 1; Text-fig. 11). The dorsal surface bore 7 rounded dorsal swells, lying dorsal to each of P3-P9 (see pl. 1, fig. 1; pl. 7, fig. 2; and pl. 10, fig. 2). The vertical diameter of the trunk, therefore, was one fourth to one fifth longer at the swells than in the remainder of the trunk. Based on the proportion between the width of the trunk and the height of the plate, which gives the same value both in dorsal and lateral preservation, the cross section of the trunk appears to be circular.

The trunk surface can be subdivided into dorsal, ventral, right and left longitudinal faces. The dorsal face is represented by the longitudinally extended soft-bodied area lying dorsal to the upper margin of the plates. The longitudinally extended and entirely soft-bodied area between the two ventral margins of the plate of a pair is referred to here as ventral face. Subdorsal specimens show that the width of the ventral face (based on the distance between the bases of the plates of a pair), corresponds to three fourths of the diameter of the trunk. The longitudinal right and left faces bear plates and their lateral borders are defined both by ventral and dorsal margin of the plates.

The external surface of the trunk is annulated with low ridges. They form triangular projections on the dorsal side (pl. 9, figs. 1-2; and pl. 18, fig. 2) as well as on the ventral (pl. 17, fig. 2), about 0.12 mm high. The annuli are evenly spaced, about 0.18 mm apart, occurring only within the areas between two successive pairs of plates. The external surface on the swells, head and rear projection appears to lack annuli. Several specimens also show the presence of small closely distributed papillae, expressed in the fossil as dark positive dots about 0.05 mm across, seen in ELRC 30012 (pl. 3, fig. 2; Text-fig. 5:1), ELRC 30061 (pl. 15, fig. 2), ELRC 30031 (pl. 15, fig. 1), and ELRC 30051 (pl. 18, fig. 1).

The annular ridges are often preserved in dark brown color, sharply contrasting with the inter-annular spaces which are yellowish. The difference in color between the annuli and the inter-annular spaces may suggest a different chemical composition, presumably with the sclerotization of the annuli stronger than in the interspaces. As an effect of the ventral curvature, the annuli are set closer on the ventral side. They appear in a lighter color and in a weaker relief on the ventral side, suggesting that the sclerotization may be lighter there than on the dorsal side.

The trunk is subdivided longitudinally into equally long subdivisions in its middle part, subdivisions becoming longitudinally shorter anteriorly and posteriorly. Each of the subdivisions 4-6 corresponds to 9% of the entire length of the animal. The subdivisions 1 and 2 are shorter, each having a length equal to 6%; and sdv3 to 8%; whereas sdv7, sdv8 and sdv9 each correspond to 7% of the entire length of the animal.

Traces of a dark, elongated band are preserved in a number of specimens, and the traces are here interpreted as the alimentary canal which extends antero-posteriorly from the anterior mouth opening as far as the rear projection. As is shown by the specimens, the canal appears not to be held in a firm position within body cavity, but shows a position variable between the trunk centre and the ventral margin. When the body was held straight, this tended to cause some elongation of the body (in its ventral part) and an increase of the anteroposterior tension. In this more strained state the canal tended to rise to a subcentral position (see pl. 6, fig. 1; pl. 16, fig. 2; pl. 18, fig. 2; pl. 19, figs. 1-2). A ventral curvature of the body appears to cause a release of the strained state and therefore a lowering of the alimentary canal into a subventral position (see pl. 6, fig. 2; pl. 11, fig. 1; pl. 15, fig. 2). The degree of tension within a body usually differs between its different sections. In anterior coiled sections, the canal usually lies subventrally, tending to shift to a subcentral position in the posterior sections if these are held more straight (see pl. 7, fig. 2; and pl. 15, fig. 2). In rare instances a short section of the gut shows a well defined mud infilling (for example in sdv 7 in NIGP 108287; pl. 7, fig. 2).

The ventral canal was an internal structure extending longitudinally and subventrally. It is only rarely preserved, and then expressed as traces of a dark or bluish gray band which is well represented only in a single specimen (Fig. 3b in Ramsköld & Hou, 1991). In the specimen both the alimentary and the ventral canal are present and the latter one occupies a position close to the ventral margin, appearing to be disconnected from the alimentary canal, but being linked to the canals which extend centrally through each of the legs.

This animal was supported by 10 pairs of elongated and unjointed legs which extend ventrolaterally from the body, each of the legs of pairs Lg1-Lg8 being based immediately underneath the plates P1-P8. The legs pairs Lg9 and Lg10 were based anteriorly and posteriorly below the P9 plates. The longitudinal spacing of the legs was equal between the middle three pairs, with distances shortening both posteriorly and anteriorly.

The legs were subcylindrical, weakly tapering distally, with the distal portion quickly narrowing. They were not differentiated in morphology but the size varies among the different leg pairs. Table 3 shows that the anterior 3 pairs usually were longest, corresponding to 16% the length of entire animal. The length of the middle four pairs was intermediate, varying from 16% to 11% the length of entire animal. The rear three pairs were both shortest and stoutest, usually with a length between 9% and 12% of the entire animal. Only a single specimen (ELRC 30009; pl. 13, fig. 2) shows the legs much longer, corresponding to 16% the length of entire animal.

The external surface of the legs was annulated with fine annuli which are evenly spaced, about 0.11-0.12 mm apart (see pl. 6, figs. 1-2; pl. 9, fig. 1; pl. 10, fig. 2; pl. 12, fig. 2; pl. 16, fig. 2; pl. 18, fig. 2). The legs in specimen ELRC 30061 shows the presence of closely distributed papillae which are expressed in the fossil as dark positive dots about

Table 3. The length of legs preserved parallel to the bedding plane (L, in mm); and the length relation of the leg (L) with entire animal (EL) in percent

		L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
NIGP	L	7.2	7.0	-	-	-	7.0	5.3	4.8	4.7	4.5
108287	L/EL	16%	16%				16%	12%	11%	11%	10%
NIGP	L	-	-	-	-	11	-	8.5	-	-	6.0
108286	L/EL					14%		11%			10%
ELRC	L	-	-	-	-	5.6	4.2	4.2	-	-	4.0
30060	L/EL					15%	11%	11%			10%
ELRC	L	-	-	-	-	7.6	-	-	-	-	-
30008	L/EL					14%					
ELRC	L	-	-	-	-	-	8.2	8.0	-	5.5	5.5
30006	L/EL						13%	13%		9%	9%
ELRC	L	-	-	-	-	-	-	6.4	4.8	-	-
30027	L/EL							13%	9%		
ELRC	L	-	-	4.3	-	4.1	-	4.7	4.7	4.7	3.5
30009	L/EL			14%		14%		16%	16%	16%	12%
ELRC	L	-	-	6.0	-	-	-	-	-	-	-
30007	L/EL			16%							
ELRC	L	-	-	-	6.7	-	-	-	-	4.2	4.2
30021	L/EL				16%					10%	10%
ELRC	L	-	-	-	-	4.8	-	-	-	-	-
30061	L/EL					13%					

0.05 mm across (pl. 15, fig. 2; Text-fig. 33). Each of the legs had a fine canal running centrally through the entire length of the leg. This canal is referred to here as the central canal. It branched out from the ventral canal of the body cavity, and is expressed in the fossil as a dark band, seen only in a few well preserved specimens (see pl. 2, figs. 1-2; pl. 6, fig. 2; pl. 19, figs. 1-2).

Each leg terminated with two claws, although they are usually either concealed by matrix or not preserved, and are observed only in some specimens (pl. 3, fig. 2; pl. 6, fig. 2; pl. 13, fig. 2; pl. 16, figs. 1-2; pl. 17, fig. 2; pl. 19, figs. 1-2). They are seen as dark, three-dimensional structures, having a wide inwardly projecting base from which a talon-shaped claw extends. The claw has an evenly curved outer edge, and is about 0.35 to 0.5 mm long., and 0.3 to 0.4 mm wide. The claws appear to attach to the inner side of the distal extremity of the legs, and have their distal spine directed adaxially with the outer edge curving to a horizontal or slightly dorsally inclined position, except for the rear pair of legs (Lg10) in which the claws were attaching to anterior side of the leg's distal end and with the distal spine directed anteriorly and slightly dorsally.

The legs were flexible and are preserved in straight, curved or twisted form, implying that the shape of the legs could be considerably modified. The legs in the anterior 9 pairs usually curve posteriorly whereas the posterior pair tends to curve anteriorly. All leg pairs Lg1-Lg10 also tend be weakly curved adaxially, with their concave side facing inward.

The rear projection of the animal is well preserved in a number of specimens. Its connection with the course of the alimentary canal usually is not clearly visible. The interpretation of the rear projection as the anal projection is to some extent conjectural. In at least one specimen (Ramsköld 1992b, fig. 1) a bluish gray line extending centrally throughout the projection is regarded here as the most posterior part of the alimentary canal. The rear projection in *Microdictyon* protrudes postero-ventrally from the margin, slightly ventral to the posterior end of the body, and is about 1 mm long and 0.5-0.7 mm wide (see pl. 1, fig. 1; pl. 6, fig. 2; pl. 7, fig. 2; pl. 9, fig. 1; pl. 10, fig. 2; pl. 12, fig. 1; pl. 13, fig. 2; pl. 18, fig. 2; and pl. 19, figs. 1-2).

The animal was armoured with nine pairs of plates along the sides of the trunk. They are convex outward, preserved either as casts of the internal surface or moulds of the external surface. The plates are composed of a roughly hexagonal meshwork, each cell encasing a circular tube. On top of the hexagonal meshwork there are numerous small spiky projections protruding from the junctions of the walls, so that each tube is surrounded by six projections. The spiky projections are preserved in a distinctly black color, sharply contrasting with the underlying hexagonal meshwork which is yellowish (Text-fig. 5:2). They are well preserved in a few specimens (ELRC 30008 and ELRC 30042), all having a subcircular base about 0.04 mm in diameter, tapering outward rapidly to a sharp apex which tends to incline dorsally.

The hexagons and the related tubes are smaller near the plate's periphery, while the upper range of size is roughly the same among the different sizes of the individuals, about 0.17 mm to 0.15 mm in P3-P9, 0.12 mm in P2 and 0.08 mm in P1.

The plates are three-dimensionally preserved, and were made of very tough matter. In most cases the rigid girdle of plates have acted as a wedge to force the opposite plate apart when the two plates of a pair were pressed upon each other under the pressure of vertical compaction. The cutting edge around the plate is usually seen as a smoothly rounded shape (see pl. 1, fig. 1; pl. 2, figs. 1-2; pl. 6, figs. 1-2; pl. 10, fig. 1; pl. 13, fig. 2). As is shown by evidence of soft deformation in the plates of ELRC 30041 (see pl. 10, fig. 1) that appear to have been buckled without evidence of breakage, the plates in *Microdictyon* were not completely mineralized. Although they might have been impregnated with apatite crystallites, the crystallites apparently lacked an interlocking fabric (Bengtson *et al.*, 1986).

As an effect of resistance against compaction, the vertically extended plates of each pair in the dorsal or subdorsal (or ventral or subventral) specimens (see pl. 2, figs. 1-2; pl. 7, fig. 1; pl. 8, figs. 1-3; pl. 10, fig. 1; pl. 14, fig. 2; pl. 15, fig. 1; pl. 16, figs. 3-4; pl. 17, fig. 1; pl. 18, fig. 1; and pl. 20, fig. 1), tend to rotate into an orientation parallel to the plane of bedding, resulting in a noticable lateral expansion of the trunk. The specimens show that rotation of the plates took their base as pivotal point, both plates of a pair rotating in the same direction, either right or left. The lateral expansion occurred on the side toward which the free (stratigraphically higher) ends rotated. The trunk margin of the opposite side did not only lack lateral expansion, but was forced to retreat.

The plates are differentiated both in size and morphology into four morphotypes referred to here as EL (elongated) form, R (round) form, OV (ovoid) form and RH (rhomboidal) form. The EL form is represented by the anteriormost pair and is characterized by a dorso-ventrally compressed elliptical form, with a ratio of length/height 5/3 (Text-fig. 10:1). The R form corresponds to pair P2, is regularly rounded, having a lenght/height ratio about 1/1 (Text-fig. 10:2). Plate pairs P3-P8 belong to the OV form, are egg-shaped, with their narrower end directed dorsally, having a length/height ratio averaging 2/3 (Text-fig. 10:3-8). The RH form of pair P9 is roughly subqudratic, with the angles situated dorsoventrally and anterioposteriorly. Except for the anterior corner which is distinctively angular, the remaining three are subrounded. The length/height ratio of the RH form (as indicated in Text-fig. 10:9), is about 1/1.

The comparative study (see Text-fig. 10) of the plates among the different individuals shows that each morphotype kept a certain fixed ratio of length against height between different growth stages of the individuals.

DESCRIPTIONS OF LATERAL OR SUBLATERAL SPECIMENS

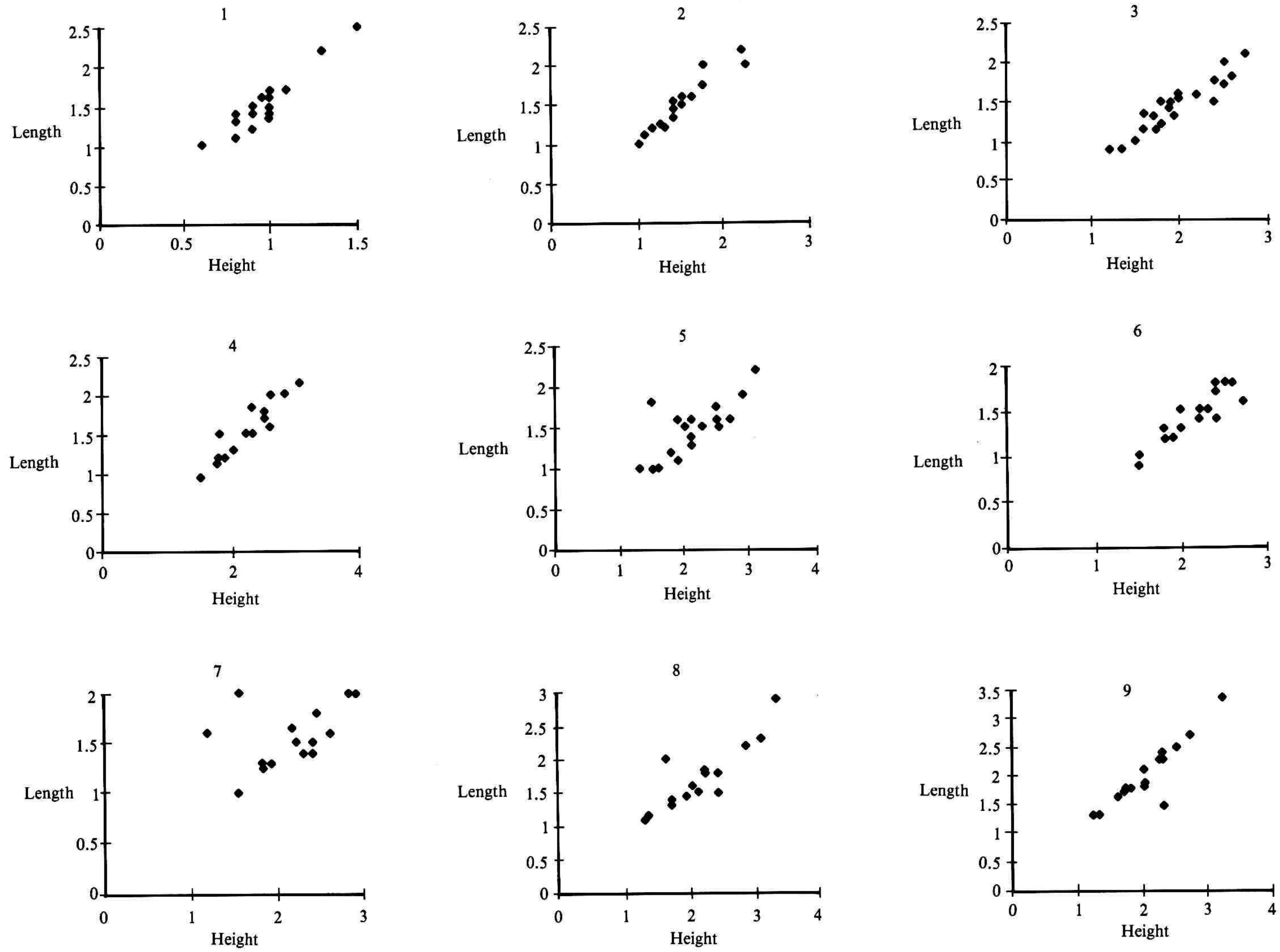
1. Holotype (NIGP 108786a, b)

(Plate 1, figure 1; Text-figure 11; Tables 4 and 5)

The holotype is one of the best preserved specimens (Chen *et al.* 1989a, pl. 1, figs. 1-2; text-fig. 5), approaching completeness. It is flattened laterally due to sedimentary compaction, but shows some visible residual relief in the plates. The specimen represents an animal which was buried with its sagittal plane roughly parallel to the bedding. Plate 1, figure 1 shows that the animal was buried in a parallel orientation but in a slightly twisted manner both horizontally and transversely. It therefore lies at slightly different levels in the matrix, and is tilted down postero-ventrally in the posterior 15 mm with a tilted angle about 17° ventrally and 4°-8° posteriorly. The body is tilted ventrally in the middle part (sdv4-sdv7), anteriorly in sdv3; and dorso-anteriorly in the head and anterior two trunk subdivisions. The length of this specimen as preserved measures about 69 mm along its dorsal margin, representing the largest individual known. The complete length of the animal before compaction is estimated to have been 76.7 mm. The head region is coiled ventrally and tilted dorsally at an angle of about 17°, as indicated by the dislocation of the two plates of P1 (calculated according to the equation $\tan \alpha = L/D$; L, length of dislocation; D, diameter of trunk). It tapers anteriorly and measures 13.1 mm along its dorsal margin, with an original length estimated to 17 mm by the equation of $13.1\ \text{mm} + 13.1\ \text{mm} \times \tan 17°$.

Body subparallel-sided, having an even diameter of 4 mm in most parts, except for the anterior two subdivisons which taper anteriorly. Dorsal margin with an undulating profile, saddles with symmetrically rounded swells situated dorsally to each of the plates of the 3rd to 9th pairs, reaching an altitude of 1 to 1.2 mm above the non-raised parts of the dorsal margin (between the saddles). Much of the external surface of the soft body appears smooth, except for the interval between the 2nd and 3rd pairs of plates which shows weak traces of annuli.

The trunk is divided longitudinally by the 9 pairs of plates into 9 subdivisions. Except for sdv5 to sdv7 which are in parallel preservation and therefore retain the original length, the anterior 4 and



Text-figure 10. Diagram showing variation of length (vertical axis) compared with height (horizontal axis) of the plate pairs P1 to P9 in differently sized individuals of *Microdictyon sinicum* collected from Chengjiang, Yunnan (in mm).

Table 4. Measurements in the holotype NIGP 108286, showing the length (SL) of the subdivisions of the body in mm; the angle of tilt of the longitudinal axis both in transverse (T°t) and in longitudinal direction (T°1); reconstructed original length (OL) in mm; and relation in length between the subdivisions and the reconstructed entire length of the animal in percent (L%); d, dorsal; a, anterior; p, posterior; v, ventral

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	13.1	4.1	4.3	5.6	6.3	6.3	6.6	5.7	4.2	3.6
T°t	12°d	12°d	0°	14°v	13°v	16°v	23°v	30°v	17°v	17°v
T°1	13°a	13°a	12°a	5°a	0°	0°	0°	0°	4°p	8°p
OL(mm)	16	5	5	6	6.3	6.3	6.6	5.7	4.5	4.2
L%	20	7	7	8	8.5	8.5	9	8	6.5	6

posterior 2 subdivisions are preserved obliquely with their length being modified (shortened) (see Table 4). The length of the subdivisions of the trunk is subequal in the middle four parts, decreasing posteriorly and anteriorly.

The rear projection is represented by traces of an elongated extension tending to tilt anteriorly into a lower bedding level, with a vague margin, being 2 mm long and 1 mm wide.

The legs are either covered by matrix, or were accidentally removed during the original preparation, so that only some of the left ones; LLg5, LLg6, LLg7, and LLg10, are completely or nearly completely preserved. The claws are only poorly preserved, present in LLg6 and LLg7. The central canal is only weakly discernible in LLg6 and LLg7.

Nine pairs of plates are present. The presence of an additional, anteriormost pair described by Chen *et al.* (1989a), is rejected by the present study because it is a poorly preserved structure consisting of a dark patch lacking plate sculpture, and of which there is no indication in any other known specimen. As an effect of the vertical compaction, the margin of each plate of a pair was acting as a sharp, hard wedge which forced the formation of a deep indentation or fracture of the opposing plate. The fracture has a smoothly rounded shape which is defined by the shape of the girdle in the opposite plate. In the specimen the split of the rock usually went through the outer surface of the nonoverlapped part of the left plates and then descended beyond the fracture and passed through the inner surface of the opposite plates. The fracture on the inner surface of the right side plate was formed by the sharp girdle of the left plate, and is indicated by a narrowly extended structure in a positive or negative relief.

The four morphotypes are well seen in this specimen. The EL form (P1) is horizontally elongated, having a length (PL) second only to the RH-form among the plates of the individual (Table 5), corresponding to 3.3% the length of the entire animal. The R-form (P2) is smoothly rounded, with a PL equal to 3% of the length of the animal. The OV-form is represented by P3-P8 which are subequal in size (Table 5), with a PH 1.3-1.5 times the length of PL and 4.2% the entire animal. The RH-form (P9) shows the longest PL among the plates of the individual while its PH length is close to but shorter than the length of PL.

Table 5. Measurements in the holotype NIGP 108286, showing the height (PH), and length (PL) of the plates; width of trunk across the PH of the plates (TWp); and across the depressed sdv (TWd); the TWp and TWd against PH in percent

	sdv1	sdv2	sdv3	sdv4	sdv5	sv6	sdv7	sdv8	sdv9
PH(mm)	1.6	2.3	3.2	3.2	3.2	3.2	3.2	3.0	2.8
PL(mm)	2.6	2.3	2.2	2.2	2.2	2.2	2.2	2.1	3.0
TWp(mm)	3.0	3.5	5.0	5.1	5.1	5.1	5.1	5.1	4.5
TWd(mm)		3.5	3.6	4.4	4.2	4.2	4.3	4.0	-
TWp/PH(%)	190	152	156	159	159	159	159	170	161
TWd/PH(%)	190	152	113	138	131	131	134	133	-

The plates are three-dimensionally preserved, but mainly the polygonal network remains. The nodes are not preserved in all plates. The tubes are only seen in P1; the largest diameter is 0.1 mm; they are smaller peripherally with the smallest observed diameter about 0.025 mm; the bottom as indicated by the inner surface of the RP1, closed by a round sheet. The size of the polygons is constant among the plates, larger in the centre and smaller peripherally, with the largest observed diameter about 0.14 mm and the smallest one 0.03 mm.

The alimentary canal is seen as a dark film, about 0.8 mm wide, being simple and straight and extending through much of the trunk, mostly in a subventral position but in a submarginal position in the anterior portion.

2. NIGP 108287

(Plate 7, figure 2; Text-figure 19; Tables 6 and 7)

The paratype (Chen *et al.*, 1989a, pl. 2. figs. 1-2; text-fig. 6) is a lateral specimen which is coiled ventrally. The coiling increases anteriorly so that the anterior part is preserved in a subcircular form. The sagittal plane, as indicated by the disposition of the plates of each pair, is twisted with its anterior portion tilted ventrally or postero-ventrally and the posterior portion in sdv7-sdv9 inclined anteriorly (Table 6). The specimen has now been prepared considerably, in particular to reveal previously unexposed legs.

The extended length of the body, as measured along the dorsal margin, is 41.6 mm long and its undeformed original length is estimated to have been about 44.5 mm. The head is elongated, with a broadly rounded front margin, expanding posteriorly in width from 1.1 mm to a width of 1.8 mm at its posterior end. The trunk is subcylindrical, with a diameter of 2.5 mm except for its anterior two subdivisions which taper anteriorly. It can be subdivided by the plates into nine subdivisions which are equally long in the middle three subdivisions, shorter in the other (Table 6).

All nine pairs of plates are present, with only the polygonal network preserved. The split passes between the left and right side plates, revealing a large part of the inner surface of the right plates. The major parts of left plates are detached. The upper range of the polygons is smallest in P1 (0.05 mm), larger posteriorly, being 0.1 mm in P2 and P3 and 0.15 mm in P4-P9. No nodes or tubes are observed in this specimen. The EL-and R-form are identical to those in holotype both in relative size and in morphology. Table 7 shows a substantial variation among the OV-form plates in morphology, varying from subcircular in P3 and P8 to a narrowly elongated form in P6.

Table 6. Measurements in NIGP 108287, showing the preserved length of the head and the subdivisions of the trunk (SL) in mm; the angle of tilt in transverse (T°t) and longitudinal direction (T°1); reconstructed original length (OL); and relation in length between the subdivisions and the reconstruced entire length of the animal in percent (L%); a, anterior; p, posterior; v, ventral

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	9.5	2.3	2.6	3.5	3.8	4.0	4.0	3.6	2.8	2.6
T°t	11°v	11°v	11°v	0°	0°	0°	0°	0°	0°	0°
T°1	0°	0°	0°	7°p	3°p	0°	0°	2°a	5°a	6°a
OL(mm)	11	2.3	2.6	3.9	4.0	4.0	4.0	3.8	3.1	2.9
L%	25	5.2	5.9	8.0	8.6	9.1	9.1	8.2	6.4	5.9

Table 7. Measurements in NIGP 108287, showing PH (height) and PL (length) of the plates, and their relation in percent (PH/PL); width of trunk across the plate-bearing areas (TWp); relation of the PH to the width of the trunk (TWp) in percent

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH(mm)	0.85	1.3	1.8	2.1	2.2	2.2	2.1	2.0	1.8
PL(mm)	1.5	1.3	1.5	1.5	1.4	1.2	1.3	1.5	2.1
PH/PL(%)	57	100	120	140	171	183	162	130	86
TWp(mm)	1.5	2.1	3.0	3.0	3.4	3.4	3.3	3.0	2.5
TWp/PH(%)	180	162	167	143	155	155	157	150	139

Seven dorsal swells are present above P3 to P9, having a height of 0.8 mm above the dorsal profile of the trunk.

Annulation is locally seen in the trunk, such as ventrally between P4 and P5, with individual annuli set about 0.2 mm apart.

The alimentary canal runs slightly ventral to the center of the trunk with exception of its anterior portion (head and the anterior two trunk subdivisions), where the canal tends to shift toward the ventral margin, to a subventral position in the head region. It is mostly indicated by vague traces of a darker film but in the subdivision 7 it is represented by a well defined, longitudinally elongated three-dimensional structure with a width of 0.3 mm. This is a rare instance of mud infilling in the gut of *Microdictyon.*

The legs are usually exposed on right side only and the left side legs were detached by splitting, but in Lg9 and Lg10 both legs of a pair are present. Legs Lgl-Lg6 appear to be longer, about 7 mm to 7.5 mm long whereas Lg7-Lg9 are short, ranging from 5.3 to 4.7 mm in length. RLgl extending anteriorly with a length of 7.2 mm; RLg2, anteroventrally extended, with a preserved length of 7 mm; RLg3 extended ventrally with its distal portion being concealed by the trunk; RLg4 and RLg5 extended ventrally, 0.7 mm wide, with their distal portion concealed by trunk; RLg6 extended ventrally, with a preserved length of about 7 mm; RLg7, preserved length 5.3 mm; RLg8, having a preserved length of 4.8 mm. Lg9 preserved in pair, LLg9 straight, 4.4 mm long, 0.9 mm wide, extended adaxially; RLg9, in a gentle curvature with concave side facing anteriorly, extended length 4.7 mm. Lg10 preserved in pair, both legs substraight with weakly concave side facing anteriorly, 4.5 mm long, 0.9 mm wide (see Table 3).

3. NIPG 108289

(Plate 5, figure 1; Text-figure 15; Table 8)

This paratype (Chen *et al.*, 1989a, pl. 3, fig. 1) is a juvenile, sublaterally compacted individual. It has a preserved length of 15 mm, representing a nearly complete trunk. The length of the entire animal is estimated to have been 23 mm. This fossil is exposed on the stratigraphically lower surface of a slab. The sagittal plane, as indicated by the dislocation of the plates of each pair, is tilted down (stratigraphically) toward the ventral side, with the angle of tilt calculated to 18°-19°. The specimen has now been prepared to reveal large, previously unexposed areas. Eight trunk subdivisions are preserved, showing an equal length in sdv3 to sdv8, shorter in sdv2 and sdv9 (Table 8).

The split passed along the lower surface of the fossil, therefore revealing a concave inner face of the left plates and a convex outer face of the right. Eight pairs of plates are present (P1 is missing) and as indicated by the dislocation of the plates, all were obliquely oriented originally (relative to the plane of bedding). The vertical compaction has forced them to reorient into a horizontal position by means of a transverse rotation with the dorsal margin moving in the direction opposite to the original slope of the sagittal plane. During the rotation, the dorsal margin of the left plates tended to push the adjacent cuticle toward the dorsal side, causing a deformation of the shape of the swells which are raised to a vertical height of about 0.6 mm to 0.8 mm above the general dorsal profile, corresponding to about 1/3 the diameter of the trunk. The trunk width across P5, P6, P7, and P9 (see Table 8), ranges from 171% to 186% times the height of the plates. In a parallel preservation, as indicated by NIGP 108287 (see Table 7), the relation between the diameter of the trunk across the swells and the height of the plates is 139% to 155%. This shows that the vertical compaction has caused an increase of the width of the trunk at P5, P6, P7, and P9 corresponding to 16% to 47% times the height of the plates.

Most of the right legs were detached by splitting and so only Lg9 is represented by both legs of the pair. The left legs are, on the other hand, usually covered by matrix, and only LLg7-LLg9 are exposed. All the legs are straight and only partially preserved, with an exception of LLg7 which is nearly complete, with traces of a claw seen at its distal end. It appears to have a parallel preservation, retaining an original length of 4 mm and a width of 0.7 mm.

The alimentary canal is expressed as traces of dark film which appear in a variable position, lying subventrally in sdv7, subcentrally in sdv6 and sdv3, and subdorsally in sdv4 and sdv6. This variable position indicates that between P6 and P3, as an effect of transverse rotation of the plates, the gut may have been forced toward the dorsal side.

Table 8. Measurements in NIGP 108289, showing the length of the trunk subdivisions (SL); the PH (height) and PL (length) of the plates; the angle of tilt (T°); trunk width across the swells (TWp) and across the depressed areas (TWd); the relation of the TWp and TWd of the trunk to the PH in percent; d, dorsal

	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.4	1.9	2.0	2.0	2.1	2.0	1.9	>1.5
PH(mm)	-	1.3	1.4	1.4	1.4	1.4	1.5	1.2
PL(mm)	-	1.1	1.0	1.0	1.0	1.0	1.1	1.3
T°	18°d	18°d	18°d	19°d	18°d	18°d	18°d	18°d
TWp(mm)	-	-	-	2.6	2.5	2.4	2.3	2.2
TWd(mm)	-	-	1.8	1.8	1.8	1.8	1.7	-
TWp/PH(%)	-	-	-	186	179	171	153	183
TWd/PH(%)	-	-	129	129	129	129	113	-

4. ELRC 30060

(Plate 5, figure 2; Plate 6, figure 2; Text-figures 4 and 17; Tables 9-11)

This is a complete specimen of an entire animal, revealed by preparation from the lower side (stratigraphically) of a slab, showing co-occurrence with an *Eldonia* in the same turbidite mud layer (see pl. 5, fig. 2).

The body is sublaterally compacted and coiled ventrally. Its sagittal plan is twisted, tilted down (stratigraphically) in posterior direction in the anterior part, dorsally in sdv3, anteriorly in sdv4-sdv7 and ventrally in its posterior part. As an effect of vertical compaction the length in the parts of the body which are buried obliquely, suffered varying degrees of modification as shown in Table 9. The preserved length of the animal measures 34.4 mm along its dorsal margin. Table 9 shows that the total amount of length reduction caused by compaction is estimated to 4.9 mm and the original length of the entire animal was therefore about 39.3 mm. Head subcylindrical, 5.5 mm long (original length 6.6 mm) (corresponding to 17% of the length of the entire animal), expanding posteriorly from 1.3 mm to a maximal width of 1.5 mm at the anterior margin of P1, with broadly rounded front margin which bears a small concave structure at a subcentral position. Trunk cylindrical, expanded posteriorly to a maximal width of about 3 mm at P3 whereas the width in the remainder of the trunk is subequal. Nine pairs of plates divides the trunk into nine subdivisions of an equal length in the middle part and the length of subdivisions is shorter both in the posterior and in the anterior three (Table 9). Seven swells are present, each lying dorsal to P3-P9, rising about 0.8-0.9 mm above the dorsal profile.

Annuli are well visible in this specimen in the area between two successive pairs of the plates, but are absent both in the head region and in the dorsal swells. They are evenly spaced, on the average 0.17 mm apart. The rear extension is preserved, about 0.8 mm long and 0.8 mm wide.

The alimentary canal is well represented by a distinct dark band extending horizontally below the ventral margin of the plates and above the ventral margin of the trunk, with a width of 0.3 mm. It appears to extend anteriorly along the ventral margin of the head region where it is very slender, about 0.1 mm wide.

All nine pairs of plates are present; the plates of each pair are only partially overlapping. The vertical compaction forced each of the plates with its sharp girdle into the opposite one, thereby forming a rounded, curving impression or fracture. Each of the plates is separated into two parts by these fractures, the overlapping and outlying parts. Because the overlapping parts of the right plates were entirely lost, the inner surface of the left plates is entirely exposed whereas all the right plates are incomplete, and preserved only with their outlying part. The polygons and tubes are smaller in the anterior two pairs, where their upper size limit is 0.05 mm and 0.08 mm, respectively. The other plates bear larger polygons and tubes, with an upper range of 0.10 mm to 0.12 mm.

Only a few legs are completely or nearly completely exposed. They include RLg5, RLg6, RLg7 and RLg10, which are substraight or gently curved with the concave side facing anteriorly, having one (RLg5, RLg7) or two visible claws (RLg10) attaching to their distal end. The distal end appears to be strongly folded with the claws facing anteriorly and extending subvertically in the posterior pair of legs. As is evidenced by RLg5, it is curved anteriorly and adaxially. The length of the legs, as indicated by those completely preserved (Table 11), differs along the body, with legs tending to be shorter posteriorly. The width of the legs is subequal (Table 11), only appearing to be slightly narrower in the anterior two pairs. Most legs are largely smooth, except for RLg5, RLg6, LLg6 and RLg7 which bear fine and evenly spaced annuli 0.07 mm apart. The central canal is seen RLg6 and RLg7, where it is represented by a dark line extending centrally along the leg.

Table 9. Measurements in ELRC 30060, showing the preserved length of the body subdivisions (SL) in mm; the angle and direction of tilt (T°) both transversely (T°t) and longitudinally (T°l) (a, anterior; p, posterior; v, ventral; d, dorsal); reconstructed original length (OL); and relation in length between the subdivisions and the reconstructed entire length of the animal in percent (L%)

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	5.5	1.6	2.0	3.0	3.0	3.0	3.2	3.0	2.6	2.3
T°t	0°	0°	10°d	21°d	22°d	17°d	0°	5°v	11°v	11°v
T°l	12°p	13°p	10°p	0°	9°a	14°a	18°a	18°a		
OL(mm)	6.6	2.0	2.4	3.0	3.5	3.7	4.1	3.9	2.6	2.3
L%	17	5	6	7.7	9	9.5	10.5	10	6.7	6

Table 10. Measurements in ELRC 30060, of PH (height) and PL (length) in the plates and their relation in percent (PH/PL); width of trunk (TW) across the plate-bearing points; and the relation of the PH against the width of the trunk in percent

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH(mm)	0.75	1.2	1.6	1.8	1.8	1.8	1.8	1.6	1.7
PL(mm)	1.25	1.2	1.15	1.15	1.15	1.1	1.15	1.3	1.8
PH/PL(%)	60	100	128	158	158	164	158	123	94
TW(mm)	1.5	1.8	2.8	3.3	3.3	3.2	2.9	2.9	2.6
PH/TW(%)	50	67	57	55	55	56	62	55	65

Table 11 Measurements in ELRC 30060, of the width (w) and length (l) both in the right (R) and in the left legs (L); relation of length of leg with that of the entire animal (EL) in percent. Bold figures indicate nearly complete preservation

	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Lg7	Lg8	Lg9	Lg10
R(w)	0.8		0.8	1.0	1.1	1.1	1.1	1.1	1	?
R(l)	>2		>2.1	>3.5	**5.6**	**4.2**	**4.2**	>1.9	>3.2	**4**
L(w)		0.8				1.1				0.9
L(l)		>2.2				>2				>3.1
(l)/EL					15%	11%	11%			10%

5. ELRC 30008

(Plate 10, figure 2; Plate 11, figure 2; Text-figure 24; Tables 12-14, 36)

This is a lateral specimen, with an extended length of 51.6 mm along its dorsal side. The original length is estimated to have been 53.7 mm. The body is coiled ventrally, with the head region strongly bent toward the rear. The head is subcylindrical, with a broadly rounded front, gradually expanding in width posteriorly, possessing a length of 8.9 mm. As indicated by the dislocation of P1, it is buried with the sagittal plane raised anteriorly at an angle of about 11°, with an original length calculated to 10.6 mm, equal to 20% of the entire length of the body. The trunk expands posteriorly in width from 1.6 mm at P1 to a maximum at P3 and then the remainder is cylindrical, with an even width of 2.9 mm to 3.0 mm. The dorsum of the trunk bears seven dorsal swells which lie dorsal to the each of P3-P9 and protrude from the dorsal profile of the trunk in a broadly rounded form, with a vertical height of 0.7 mm to 0.8 mm above P3 to P7, shorter above P8 and P9, about 0.5 mm.

The trunk is longitudinally subdivided into 9 subdivisions by the plates. The two plates of each pair overlap entirely in most parts of the trunk (P3-P9), suggesting that the sagittal plane in this part of the trunk is buried parallel to the plane of bedding. Its longitudinal length was not affected by vertical compaction, and is therefore equal to the original length. The length of the subdivisions as shown in Table 12 is longer in the middle part of the trunk, shorter both anteriorly and posteriorly.

The rear projection is well shown by a brown film which extends posteriorly from the subventral margin of the rear end of the body. It is 1 mm long and 0.7 mm wide.

Annuli are present on the surface in small areas of trunk, set about 0.2 mm apart (pl. 11, fig. 2).

The split of the rock was passing either along the outer surface of the left plates or traveling between the plates of a pair, revealing entirely the outer convex surface of the left plates in P2, P3 and P5. The left ones in the other plate pairs were removed, with the inner side of the right plates being largely exposed. The spiky nodes are well seen in P2, P3 and P5 where they are preserved as black and three-dimensional structures in a sharp contrast

Table 12. Measurements in ELRC 30008, showing the preserved length of the body sections (SL) in mm; the angle and direction of tilt both transversely (T°t) and longitudinally (T°l); reconstructed original length (OL); and relation in length between the subdivisions and the reconstructed entire length of the animal in percent (EL); the vertical width of trunk at depressions (TWd) and across the PH of the plates (TWp); p, posterior

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	8.9	2.8	3.3	4.3	4.6	4.9	4.9	3.8	3.5	2.8
T°t	0	0	2°d	0	0	0	0	0	0	0
T°l	10°p	10°p	0	0	0	0	0	0	0	0
OL(mm)	10.9	3.2	3.2	4.3	4.6	4.9	4.9	3.8	3.5	2.8
EL(%)	20	6	6	8	9	9	9	7	7	5
TWd(mm)	-	2.2	3.0	3.0	3.0	3.0	3.0	3.0	3.0	-
TWp(mm)	-	2.2	3.0	3.6	3.6	3.8	3.6	3.5	3.5	3.5

with the other parts of the plates which are light yellowish (Text-fig. 5:2). The polygons and associated tubes are smaller in the posterior two pairs. They have a largest diameter of 0.07 mm in P1, 0.1 mm in P2, and 0.15 mm in the other pairs of plates. The lower size is subequal among the plates and measures about 0.02mm. The dimensions of the plates and their relation with the diameter of the trunk are shown in Table 13.

The legs are mostly preserved in gently curved or twisted form with the concave side facing anteriorly. The legs of each pair diverge distally and are preserved obliquely to the bedding except for leg RLg5 which is in a parallel preservation retaining an original length of 7.6 mm, corresponding to 14% of the entire animal in length. Table 14 shows that the width of the legs differs along the trunk, appearing narrower in the anterior four pairs. The surface in few legs only (LLg6 and LLg10) bears evenly spaced fine annuli, about 0.08 mm apart.

Table 13. Measurements in ELRC 30008, of PH (height) and PL (length) in the plates, and their relation in percent (PH/PL); trunk width (TWp) across the PH of the plate and the relation of the PH against the width of the trunk in percent

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH(mm)	1	1.7	2.3	2.3	2.3	2.3	2.3	2.3	2.2
PL(mm)	1.5	1.6	1.6	1.5	1.5	1.5	1.5	1.5	2.1
PH/PL(%)	67	106	144	153	153	153	153	153	95
TWp(mm)	1.6	2.7	3.6	3.6	3.6	3.5	3.5	3.5	3.5
TWp/PH(%)	160	159	157	157	157	152	152	152	159

Table 14. Measurements in ELRC 30008, of the width (w) and length (l) both in the left (L) and right legs (R) in mm; bold figure indicates that the complete length is preserved; italics indicate that the leg is preserved obliquely

	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Lg7	Lg8	Lg9	Lg10
L(w)				1.2		1.2		1.2		1.2
L(l)				6.8		*5.1*		>4.5		>4
R(w)	0.6	0.7	0.7		1.2	1.2	?			
R(l)	2	>6	>3		7.6	4	>3.2			

6. ELRC 30006

(Plate 19, figures 1-2; Text-figures 42 and 43; Tables 15-17)

This specimen is laterally compacted, represented by both part (pl. 19, fig. 1; Text-fig. 42) and counterpart (pl. 19, fig. 2; Text-fig. 43), with a preserved length of 46 mm including a complete trunk and a posterior part of the head region. As is shown by the disposition of the plates of a pair, the body was buried with the sagittal plane parallel to the bedding, therefore retaining the original length of the trunk sections. These are of equal length in the middle three subdivisions (sdv4-sdv6), shorter both posteriorly and anteriorly (Table 15). The entire length of the animal, as extrapolated from the length of the preserved parts, was about 61 mm.

The trunk is roughly parallel-sided in its middle part, with an even width of 3.2 mm at the midlength between two successive pairs of plates in the middle three subdivisions, increasing to 4.0 mm at the plate-bearing points P4-P7 (Table 16). The dorsal swells are raised to a vertical height of about 0.7 mm above the dorsal margin between the swells. The posterior margin of the body is broadly rounded and defined mainly by the posterior swell which extends both posteriorly and ventrally to join the rear extension at midlength of the posterior margin.

The rear projection is well preserved in the counterpart, extending posteriorly from the lower half of the posterior margin of the body adjacent

Table 15. Measurements in ELRC 30006, showing the length (SL) of the body subdivisions (sdv)

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	3.0	3.2	4.3	5.3	5.5	5.5	4.5	4.0	3.3

Table 16. Measurements in ELRC 30006, showing the trunk diameter at the plate-bearing points (TWp) and at the midlength between two successive pairs of plates (TWd); all measurements in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
TWp	2.6	2.8	3.4	4.0	4.0	4.0	4.0	3.9	3.7
TWd	2.7	2.9	3.1	3.2	3.2	3.2	3.0	2.9	

to the posterior swell anteriorly and to the posterior legs ventrally. It is 1.5 mm long and 1.5 mm wide.

All the legs Lg1-Lg10 are present; Lg2-Lg6 having the right side legs of a pair exposed while Lg1 and Lg7-Lg10 show both. They are extending straight from the trunk, with well defined margins. The distal part is usually coiled, with the concave side facing toward anterior (LLg10), or posteroadaxially (RLg7, LLg7) and anteroadaxially (RLg4). The central canal is visible in several legs, running along the leg either subcentrally (RLg6, LLg8, RLg8), or submarginally (RLg9, RLg10, LLg10). In Lg7 it tends to drift from one side to the other. The legs have an even width of 1.2 mm in Lg5-Lg10 but pairs Lg1-Lg4 are more slender, about 0.7 mm wide. The length differs among the legs, the posterior three being shorter (Table 17).

The claws are visible in RLg4, RLg6, RLg7, LLg7, RLg8, LLg8, RLg10 and LLg10. Legs of Lg7 appear to be flexed dorsally and adaxially near the distal end. As an effect of the vertical compaction, the distal part is therefore preserved lying on top of the leg, with two claws attaching to its tip. They are of the same size, both seen from the outer edge with the spine directed dorsally, about 0.34 mm in width at the base and 0.32 mm in length. RLg10 has an anteriorly bent distal portion with a well preserved claw attached to its termination. The claw is laterally compacted and expressed in black color with positive relief, showing a broad base 0.34 mm wide and a recurved spine 0.4 mm long. The color of the claw is much lighter on its base and increasingly darker distally, suggesting that the color change is due to a change in chemical composition. Sclerotization is possibly increasingly stronger from the base of the claw toward its distal end.

The alimentary canal is expressed as traces of a dark band extending longitudinally and subcentrally for most of the body length, but shifting to a subventral position in the ventrally curved trunk portion anterior to P4.

Table 17. Measurements in ELRC 30006, showing the width (w) and the length (l) of the legs, in mm

	LLg4	LLg5	LLg6	LRLg7	LRLg8	RLg9	RLg10
(w)	1.2	1.2	1.25	1.25	1.25	1.2	1.2
(l)		7.4	7.4	7.2	5.6	5.5	5.5

7. ELRC 30027

(Plate 9, figures 1-2; Text-figure 22; Tables 18-19)

It is represented by both part (pl. 9, fig. 1; Text-fig. 22) and counterpart (pl. 9, fig. 2). The main part of the fossil is exposed on the lower surface of a slab which is assigned as part. The individual is preserved in substraight form but is coiled in its anterior portion. The dislocation of the plates of a pair suggests that the animal was buried sublaterally, with its sagittal plane tilted down (stratigraphically) toward ventral side. The entire length of the trunk measures 39 mm and the entire length of the animal is estimated to have been 51 mm. The trunk is subparallel-sided with a larger width in the middle part, smaller both posteriorly and anteriorly (see Table 19).

Except for P2 which are missing, all plates are present. The split of the rock was passing the polygonal framework along the outer face of the right and inner surface of the left plates. The outer layer of the plates is either conceiled within the matrix or detached by splitting. The vertical and horizontal diameter of each pair of the plates is given in Table 18. Plate RP6 is interesting in showing a division into two separate plates; ventrally a larger, and dorsally a smaller, almost circular one. The two plate components are in

Table 18. measurements in ELRC 30027, showing height (PH) and length (PL) of the plates, in mm

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH	1.0	-	2.1	2.7	2.5	2.5	2.5	2.3	2.0
PL	1.5	-	1.5	1.7	1.6	1.7	1.7	1.7	2.3

Table 19. Measurements in ELRC 30027, showing the length (SL); trunk width across at the plate-bearing point (TWp) and at mid-length between two successive pairs of the plates (TWd); all measurements in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	3.2?	3.2?	3.7	4.9	5.0	4.5	4.1	3.5	3.0
TWp(mm)	2.0	-	-	4.0	4.0	4.0	3.7	3.6	3.6
TWd(mm)	2.0	-	-	3.1	3.2	3.1	3.0	3.0	-

immediate contact, but appear to be functionally separate plates. LP6 is normal, and the condition in RP6 is regarded as pathological.

The trunk bears evenly spaced annuli in the areas between each two successive pairs of plates. The annuli are set 0.2 mm-0.3 mm apart and are sharply ridged; most of them extend continuously across the trunk, although they are weak in the central part. The length of the trunk subdivisions between the plates is subequal in sdv4-6, shorter both anteriorly and posteriorly (Table 19).

Seven dorsal swells are present and raised to a vertical height of about 0.8 mm above the general dorsal profile. The rear projection is vaguely outlined, extending posteriorly from the subventral margin of the posterior face.

The legs are well exposed in the posterior portion of the trunk. The 7th pair is gently curved with its concave side facing posteriorly and was buried parallel to the plane of bedding, retaining an original length of 6.4 mm which corresponds to 12.5% of the entire length of the animal. The 8th pair is represented only by LLg8 which is extended straight, about 4.8 mm long and 1.2 mm wide. The legs in Lg9 and Lg10 are straight, 1.2 mm wide and 4.0 mm long in Lg9 and 3.8 mm in Lg10. Annuli are shown on the surface of Lg7-Lg10 and they are evenly spaced, set 0.06 mm apart.

The alimentary canal is represented by a straight black band about 0.3 mm wide, extending longitudinally in a variable position, lying subventrally in its anterior and subcentrally in its posterior portion.

8. ELRC 30015

(Plate 18, figure 2; Text-figure 41)

This is the posterior part of an adult which was buried laterally. It has a preserved length of 11 mm representing the posterior three subdivisions and three pairs of the plates. The length of the subdivisions measures 4.2 mm in sdv7, 3.4 mm in sdv8 and 2.9 mm in sdv9. The entire length of the animal is estimated to have been 47 mm. Annuli are preserved in a distinctive manner in areas between two successive pairs of plates. Each of the ridged annuli tend to form a triangular projection on the dorsal margin, with a height of 0.15 mm above the dorsal margin. They are evenly spaced, set about 0.2 mm apart.

All the exposed legs are annulated and kept straight. LLg8 and LLg9 are both parallel to the plane of bedding, retaining a length of 5.0 mm in LLg8 and 4.3 mm in LLg9, with an equal width of 1.2 mm. LLg10 and RLg10 are gently curved with the concave side facing anteriorly, having an extended length of 4.2 mm.

The alimentary canal is preserved both in sdv7 and sdv8, in a subcentral position. The rear projection extends posterodorsally from the subventral part of the rear margin of the body. It is about 1.5 mm long and 1.0 mm wide.

9. ELRC 30009

(Plate 13, figure 2; Text-figure 29; Tables 20-22)

This is a lateral specimen preserved in a curved form with a length of 30.1 mm (along the dorsal margin). The sagittal plane was tilted dorsally both in the head and in sdv1-sdv2, whereas it was tilted ventrally in most of the trunk posterior to P4. The head has a preserved length of about 4 mm, expanding in width posteriorly from 1.2 mm to 1.4 mm. The trunk widens posteriorly in its anterior two subdivisions and is then parallel-sided. It is divided into 9 subdivisions which are widest in the middle part of the trunk and narrower both anterorly and posteriorly (Table 20).

All nine pairs of plates are present; the split of the rock passed either through the framework of the right plates or the inner surface of the left ones. The external sculpture is, therefore, not preserved. The dimensions of the plates are shown in Table 21.

Annuli are present in the areas between two successive pairs of plates, evenly spaced 0.15 mm apart. The rear projection is incompletely preserved, about 0.5 mm long and 0.5 mm wide. The alimentary canal is preserved as a black band extending longitudinally, at one third of the

Table 20. Measurements in ELRC 30009, showing the length of the trunk subdivisions (SL) and the width of the trunk across the plate-bearing point (TWp) and the depressed sdv (TWd); all measurements in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.9	2.1	2.7	2.8	3.0	2.9	2.6	2.35	1.9
TWp(mm)	1.8	2.2	2.5	2.6	2.6	2.8	-	-	-
TWd(mm)	-	-	2.3	2.3	2.3	-	-	-	-

Table 21. Measurements in ELRC 30009, showing PH(height) and PL (length of the plates in mm

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH	0.8	1.4	1.9	1.9	1.9	1.9	1.8	1.9	1.7
PL	1.3	1.4	1.4	1.4	1.4	1.4	1.3	1.4	1.8

Table 22. Measurements in ELRC 30009, showing the length (1) and the width (w) of the legs of the right (R) and the left sides (L), in mm (bold numbers indicate parallel preservation of the entire leg; italics indicate oblique preservation of entire leg; plain style means incompletely preserved)

	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Lg7	Lg8	Lg9	Lg10
R(1)	-	-	*4.3*	-	*4.1*	-	-	-	-	*3.8*
R(w)	-	-	**0.7**	-	*0.8*	-	-	-	-	**0.8**
L(1)	-	3.7	-	1.0	-	3.5	**4.7**	**4.7**	**4.7**	-
L(w)	-	**0.7**	-	**0.7**	-	**0.8**	**0.8**	**0.8**	**0.8**	-

diameter from the ventral margin. The gut appears to terminate posteriorly at the posteroventral face of the rear extension.

The legs of the right side were largely lost with the exception of RLg5 and RLg10 which are completely preserved (Table 22). RLg5 is gently curved, with the concave side facing anteriorly. RLg10 is annulated and weakly curved with the concave side facing anteriorly, extending posteriorly with a length of 3.8 mm. Papillae are present on RLg3, RLg5, and RLg10. Seven left legs are present and largely kept straight except for LLg2 which extends posteriorly. A claw is visible at the distal end in legs RLg5, LLg7 and RLg10.

10. ELRC 30007

(Plate 6, figure 1; Text-figure 16; Table 23)

This is a sublaterally preserved specimen, exposed on the lower surface (stratigraphically) of a slab. Judging from the dislocation of the paired plates, it was buried with the sagittal plane tilted down (stratigraphically) toward the ventral side with an angle of tilt ranging between 10° and 12°. It has a preserved length of 30 mm (measured along its dorsal margin) representing a nearly complete head and the anterior seven subdivisions of the trunk. Except for the head region which is tilted down anteriorly at about 8°, the longitudinal axis in the remaining sections is parallel longitudinally to the plane of the bedding, having a length identical to the original. Based on the length of the subdivisions (Table 23), the original length of the entire animal is estimated to have been 38 mm.

The alimentary canal is expressed by a dark band which extends subcentrally in most parts of the trunk.

Table 23. Measurements in ELRC 30007, showing the length of head and trunk subdivisions (SL); the angle of tilt of each subdivision (T°); v, ventral; trunk width across the plate-bearing point (TWp) and the depressed trunk areas (TWd); the height (PH) and length (PL) of the plates; the relation of trunk width (both TWp and TWd) against the height of the plate in percent

	hd	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7
SL(mm)	5.6	2.1	2.2	2.8	3.1	3.4	3.4	3.1
T°	12°v	12°v	10°v	10°v	10°v	10°v	9°v	8°v
TWp(mm)		2.2	2.6	3.4	3.7	3.7	3.7	3.7
TWd(mm)				3.2	3.2	3.2	3.2	3.2
PH(mm)		0.8	1.3	1.9	2.2	2.3	2.3	2.2
PL(mm)		1.4	1.3	1.4	1.5	1.5	1.5	1.4
TWp/PH(%)		275	200	179	169	161	161	169
TWd/PH(%)				168	145	139	138	145

Annulations are present in areas between two successive pairs of plates. They are set 0.1 to 0.2 mm apart and are expressed as transversely extended, raised ridges which appear to be distinctive both near the dorsal and ventral margin but becoming fainter toward midlength of the annulations. The left legs were entirely lost during the split of the rock, so that only the right ones in Lg1-Lg6 are present. The legs are narrower in the anterior pair and tend to be wider posteriorly; having a width of 0.65 mm in Lg2, 0.7 mm in Lg3, 0.9 mm in Lg4 and 1.1 mm in Lg6. They are either incomplete in RLg4-RLg6 or partially covered by matrix or body in RLg1 and RLg2, but RLg3 is nearly completely preserved, having a length of 6 mm corresponding approximately to 16% of the length of animal. The external surface of the legs bears visible fine annulations.

11. ELRC 30017

(Plate 11, figure 1; Text-figure 25; Table 24)

The specimen is curved ventrally in a semicircular form in its anterior portion. The coiling decreases posteriorly so that the posterior portion of the trunk is nearly straight. The length of the specimen, as measured along the dorsal margin, is 29 mm, representing the head and the posterior 6 subdivisions of the trunk. The plates of each pair, which overlap almost entirely, suggest that the animal is in parallel preservation, and therefore retaining the original length. The complete length of the animal is estimated to have been 40 mm, based on the length of the trunk sections (Table 24).

Table 24. Measurements in ELRC 30017, showing the length of the preserved subdivisions of the body (SL), in mm

	head	sdv1	sdv2	sdv3	sdv4	sadv5	sdv6
SL(mm)	7.0	2.3	2.5	3.4	3.6	3.6	3.6

The head is completely preserved, having a length of 7 mm (along the dorsal margin), corresponding approximately to 18% of the entire length of the animal. It is subparallel-sided, tapering anteriorly from 1.4 mm to 1.2 mm with a broadly rounded anterior end. A structure interpreted as associated with the mouth opening is expressed as a dark brown spot, 0.1 mm wide and situated at the center of the front margin. The trunk is subcylindrical, with an even diameter (across the depressed area of the trunk) of 2.3 mm in sdv4 to sdv6 and tapering anteriorly in the anterior three subdivisions. The dorsal margin is undulating, with the symmetrically rounded swells situated dorsally to each of the plates of the 3rd to 7th pairs, reaching a height of 1.2 mm to 1.5 mm above the non-raised parts of the dorsal margin.

Six pairs of plates are present. The plates of each pair are extensively overlapping and each plate consists of a broad overlapping part and an extremely narrow outlying part. The split of the rock usually went through the outlying part in both the outer surface of the left plates and inner surface of the right ones, but it usually passed along the intermediate or inner part of the left plates in their overlapping part.

Much of the external surface of the soft body appears smooth, except for the ventral area of the intervals in sdv1-sdv3 which show annuli between the successive pairs of plates.

The left legs were largely lost during the split of the rock, so only the right ones and a distal part of LLg2 are present. The legs in Lg2 and Lg3 are nearly complete.

The alimentary canal is seen as a dark film, being simply straight and extending through the entire length of the trunk and posterior portion of the head region in a subventral position except for the anterior half of the head region, where it tends to be directed toward the center of the body to connect with the inferred mouth opening.

12. ELRC 30005

(Plate 20, figure 2; Text-figure 45; Table 25)

This is an unique specimen in that it is gently curved dorsally. It is sublaterally compacted and the split of the rock went through the stratigraphically lower surface of the fossil, which retains a preserved length of 24 mm, representing a major part of the trunk. The sagittal plane, as indicated by the dislocation of the plates of each pair, is inclined relative to the plane of bedding both anteriorly and ventrally (see Table 25).

As an effect of the vertical compaction, the original lengths of the trunk subdivisions are shortened. The original length of the entire animal can be estimated to have been 53 mm, based on the

Table 25. Measurements in ELRC 30005, showing the length of the trunk subdivisions (SL); the angle of tilt both in transverse (T°t) and longitudinal direction (T°1); reconstructed original length of the trunk subdivisions (OL); v, ventrally; a, anteriorly

	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	3.9	3.7	3.9	3.9	3.2	3.2	2.5
T°t	15°v	15°v	7°v	7°v	7°v	-	-
T°1	6°a	10°a	14°a	14°a	14°a	-	-
OL(mm)	4.2	4.3	4.8	4.8	4.0	-	-

calculated original length of the trunk subdivisions.

Six pairs of plates are present, with only the polygonal network preserved. The split passed along the concave inner face of the right plates and the convex outer face of the outlying part in the left plates.

The left legs were largely removed during the split of rock, so only the right ones are present except for LLg10 which is preserved. The legs are gently curved with the concave side facing anteriorly in Lg10 but posteriorly in Lg6 to Lg8. RLg5 is bent in a S-form. Traces of claw(s) are seen at the distal end of RLg5, RLg10 and LLg10.

The alimentary canal is represented by a dark brown band extending subcentrally through most of the body.

Annuli are seen on the outer surface of the soft-bodied areas between two successive plates; they are distinct in the dorsal area, but becoming fainter ventrally. This specimen shows clearly the accordion-like function of the annuli.

13. ELRC 30016

(Plate 12, figure 2; Text-figure 28; Table 26)

The specimen represents an anterior portion of an adult, being laterally compacted. It is coiled ventrally with the curvature increasing anteriorly. The preserved length measures 44 mm, representing a nearly complete head and the anterior 6 trunk subdivisions. The entire length of the animal, as indicated by the length of the subdivisions (Table 26), is estimated to have been 60 mm. The head is gently curved and incomplete anteriorly, with a preserved length of 7 mm. The trunk has a width of 3.2 mm, tapering anteriorly from 3.2 mm to 1.9 mm in its anterior two subdivisions. The dorsal swells are raised to a vertical height of about 1.9 to 2.20 mm.

Table 26. Measurements in ELRC 30016, showing the length of the body subdivisions (SL); and the trunk width both across the swells (TWp) and the depressed areas (TWd)

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6
SL(mm)	7.0	3.1	3.5	4.4	5.1	5.4	5.1?
TWp	-	1.9	2.7	3.7	-	3.7	4.0
TWd	-	-	-	?	3.2	3.2	3.2

Six pairs of plates are present; the split passed between the two plates of a pair. The external sculpture is not preserved.

Annuli are present in the areas between two successive pairs of plates, spaced evenly, set about 0.2 mm apart. The legs are either kept straight (LLg3, RLg5, RLg6 and RLg7) or curved with concave side facing anteriorly (LLg2, LLg4 and RLg4). All legs are incompletely exposed, with a width of 1.3 mm in Lg5-Lg7 and 1.0 to 1.1 mm in Lg2-Lg4. Annuli are seen in LLg2, LLg4, RLg5 and RLg6.

14. ELRC 30021

(Plate 16, figures 1-2; Text-figures 34-35; Tables 27-28)

The specimen is represented by part (pl. 16, fig. 2) and counterpart (pl. 16, fig. 1). The part has a preserved length of 18 mm representing the posterior five subdivisions whereas the counterpart preserves an anterior portion of the body including the head and anterior four trunk subdivisions. The sagittal plane, as indicated by the degree of the dislocation of the plates of each pair, is subparallel to the plane of the bedding. The extended length of the entire animal measures 42.5 mm. It is straight except for its head region which is curved ventrally in a semicircular form, with a length of 12 mm (measured along the dorsal margin). The trunk is 30.4 mm long and subdivided into 9 subdivisions which are equally long in the middle three, but shorter both anteriorly and posteriorly (Table 27).

The external surface of the body is mostly smooth, annuli are present only in a few areas of sdv2 and sdv3.

Along the dorsal margin of the specimen there is a longitudinal edge, with a visible three-dimensional relief of about 0.3 mm, corresponding

Table 27. Measurements in ELRC 30021a-b, showing the length of each subdivision of the body (SL) and relation of the length of each subdivision with the entire length of the body (EL) in percent

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	12	2.3	2.8	3.5	4.1	4.1	4.1	3.5	3.1	2.9
SL/EL(%)	28	5	6.5	8	9.5	9.5	9.5	6.5	7	6.7

to one tenth of its original thickness. This indicates that the compaction ratio of the soft body is roughly equal to the compaction ratio of the surrounding fine mud.

In most leg pairs only one of the legs is present, but in pairs Lg4, Lg7, Lg8 and Lg10 both legs can be seen. Lg10 is extended ventrally, with its distal portion gently curved with the concave side facing both anteriorly and adaxially whereas the concave side of the distal portion in Lg9 and Lg8 are facing adaxially. Both legs in the 7th pair are curved with concave side facing posteriorly. The left legs in Lg5 and Lg6 are only partially preserved. The right leg in Lg4 is curved both adaxially and anteriorly. Each leg bears two claws which are expressed as dark, three-dimensional structures and seen at the termination of the left legs Lg4, Lg5, Lg9 and Lg10 and in the right leg Lg10. The legs are about 4.2 mm long in the posterior pairs, being longer anteriorly with a length of 6.7 mm in Lg4 and Lg5 (Table 28). Annuli are present in RLg4, RLg5, RLg6 and RLg8.

All nine pairs of plates are present, with only the polygonal network preserved. The split passed between the left and right side plates, revealing a large part of the inner surface both in the left plates of the part and in the right plates of the counterpart.

Table 28. Measurements in ELRC 30021a-b, showing length (l) and width (w) of the legs of the right (R) and left (L) side, in mm

	Lg4	Lg5	Lg6	Lg7	Lg8	Lg9	Lg10
L(l)	-	-	-	4.2	4.2	4.2	4.2
L(w)	-	1.2	1.2	1.1	1.1	1.2	1.2
R(l)	6.7	6.7	-	4.2	-	-	-
R(w)	1.1	-	-	1.1	-	-	-

15. ELRC 30061

(Plate 15, figure 2; Text-figure 33; Table 29)

This is a lateral specimen which is curved ventrally in a semicircular form. The curvature increases anteriorly. The sagittal plane, as indicated by the dislocation of the plates of each pair, is gently inclined ventrally with an angle of tilt ranging from zero to 11°. The extended length of the body, as measured along the dorsal margin, is 38.7 mm long. The head is coiled into a semicircle, with a broadly rounded front margin. The trunk is subcylindrical, having an even diameter of 2.1 mm in its posterior six subdivisions. It can be divided into nine subdivisions which are equally long in the middle three subdivisions, shorter both posteriorly and anteriorly (see Table 29).

Table 29. Measurements in ELRC 30061, showing the length of the body subdivisions (SL) and the length relation between the body subdivisions and the entire animal (EL) in percent

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	6.8	2.3	2.6	3.1	3.5	3.6	3.5	3.2	3.0	2.3
SL/EL(%)	18	6	7	8	9	9	9	8	8	6

There are papillae are present both on the legs (RLg5-RLg7) and the trunk (sdv3-sdv5). They are closely distributed and expressed in the fossil as dark positive dots about 0.05 mm across.

The legs are usually exposed on the right side whereas the left side is covered by matrix, with the exception of Lg8, of which both legs are present. The legs are straight, directed ventrally, about 0.6-0.7 mm wide; Lg5 appears to be nearly completely preserved, with a length of 4.8 mm which corresponds to 13% of the length of the entire animal.

The alimentary canal is preserved as a distinct dark band, running subventrally through most of the trunk and the head region, with an exception of the posterior portion of the trunk where it lies subcentrally.

16. ELRC 30001

(Plate 12, figure 1; Text-figures 26-27; Table 30)

This specimen is a laterally compacted, medium-sized individual which is represented by the part (pl. 12, fig. 1; Text-fig. 26) and counterpart (Text-fig. 27). It is curved ventrally, having a length of 35.1 mm (measured along its dorsal margin). The head is smooth externally and curved ventrally, with an extended length of 4.1 mm. The trunk subdivisions have an equal length in sdv4-sdv7, shorter both anteriorly and posteriorly (Table 30). Annuli are seen only in sdv3 (both in part and counterpart) and sdv5 (only in counterpart).

All nine pairs of plates are present; the split passed between the two plates of each pair,

Table 30. Measurements in ELRC 30001, showing the length of the body sections (SL) and the relation of the length of each section with the entire length of the animal (SL/EL) in percent

	hd	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	4.1	1.8	2.1	2.5	2.9	3.0	3.1	3.0	2.6	2.3
SL/EL(%)	13	6	7	8	8.3	8.6	8.9	8.6	7.4	6.6

revealing the inner face of the framework without the external surface being preserved.

The legs are preserved in varying stances, and are kept straight in LLg5; curved with concave side facing anteriorly in RLg2, LLg6, RLg9 and LLg10; posteriorly extended in LLg7, RLg7, LLg8; and extended anteriorly in RLg1. LLg5 is nearly completely preserved, with a length of 4.1 mm. Traces of the central canal are seen only in LLg5 and RLg6 in the counterpart.

The alimentary canal is expressed as a dark film extending subcentrally through the entire length of the trunk.

The rear projection is vaguely outlined, with a length of 0.8 mm and a width of 0.6 mm.

17. ELRC 30010

(Plate 17, figure 2; Text-figure 39)

This is a laterally compacted specimen with a preserved length of 10.5 mm, representing the posterior four subdivisions. These measure 3.2 mm in sdv6, 3.0 mm in sdv7, 2.7 mm in sdv8 and 2.5 mm in sdv9. The entire length of the body is estimated to have been 38 mm. The preparation passed along the stratigraphically lower surface of a slab, revealing the convex outer face of the outlying part of the right side plates and the entire inner face of the left side plates. Dislocation of the two plates of a pair indicates that the aminal was buried with the sagittal plane tilted ventrally at an angle of 7°.

The legs of the right side are detached by the split, so only the left legs are present. They are kept straight, extending ventrally with one or two claws attaching to their distal end. All the claws are curved with their distal end directed both anteriorly and adaxially. The external surface bears visible fine transverse annulations both in the legs (LLg6-LLg9) and in the areas between two successive pairs of plates in sdv6-sdv8. The annulations are ridged, forming triangular projections on the ventral margin in sdv6. The alimentary canal is a dark film extending subcentrally.

DESCRIPTIONS OF SUBDORSAL SPECIMENS

18. ELRC 30012

(Plate 2, figures 1-2; plate 3, figure 2; Text-figure 12; Tables 31-34)

This is a subdorsally compacted individual. The body was ventrally curved in the sediment, and as an effect of compaction, the morphology and spacing of the body parts are modified. The compacted length of the body measures 28.6 mm whereas the original length of the entire animal, as estimated from the cumulated calculated lengths of the subdivisions of the body, is at least 35 mm long, more than 6.4 mm of the length being lost due to oblique preservation (Table 32). As is indicated both by the length difference between the two legs of a pair and the dislocation of the plates of a pair, the sagittal plane is tilted toward the right side. When the animal was buried, the plates were subvertically oriented and the fossil evidence shows that they were not deformable. The vertical compaction appears to have acted to force the subvertically oriented plates of each pair to reorient themselves into a horizontal position by means of a transverse rotation with the free dorsal margin moving in the direction opposite to the slope of the sagittal plane. The ventral margin of the plates that played the role of center of rotation, is apparently preserved in an unchanged position. The distance between the ventral margins of a pair of the plates is therefore generally identical with the width of the ventral face of the soft body. The ventral width, as indicated by the distance between the plates of a pair (Table 31), is broadest in the middle part of trunk, decreasing both anteriorly and posteriorly. As is indicated both by the size of plates and the distances between each two successive pairs of plates, the present specimen represents an animal identical in size to ELRC 30060. The dorsoventral diameter of trunk in the present specimen is assumed to be roughly identical; the measurements from ELRC 30060 serve as figures of reference for the present specimen. The ventral face of the body is estimated to have a width corresponding to 48-57% of the

Table 31. Measurements in ELRC 30012, showing the distance between the ventral margins of the two plates of each pair (VW); values from the identically sized ELRC 30060 for the dorsoventral trunk diameter at the plate-bearing point (TWp) and at the midlength between two successive pairs of plates (TWd); the ratio (in percent) between the ventral width and the dorsoventral diameter at the plate-bearing points (VW/TWp) and at midlength between two successive pairs of plates (VW/TWd) respectively

	P1	P2	P3	P4	P5	P6	P7	P8	P9
VW(mm)	0.9	1.2	1.5	1.7	1.8	1.7	1.6	1.6	1.3
TWp(mm)	1.8	2.6	3.1	3.2	3.1	3.1	2.8	2.8	2.6
TWd(mm)	-	-	2.5	2.5	2.5	2.4	2.3	2.1	2.1
VW/TWp(%)	50	53	48	55	58	55	57	57	50
VW/TWd(%)	-	-	60	68	72	71	70	76	62

dorsoventral trunk diameter at the sclerite-bearing point and to 60-76% of the trunk diameter between the dorsal swells.

The dorsal surface is strongly flattened, without any indication of annulation. Instead, there are dark brown papillated structures present, each about 0.05 mm in diameter. They are closely spaced without showing evidence of an alignment pattern.

The trunk was buried in a curved form. As an effect of subdorsal compaction, the anterior and posterior portions were buried at varying angles to the plane of bedding, and were altered in length whereas the middle portion was parallel to the bedding plane, and thus retains the original length. Table 32 shows the longitudinal length of the nine subdivisions of trunk. The comparison with the calculated original length of each of the subdivisions in ELRC 30060 (OL in Table 32), shows that the length is identical or closer to the original in the middle portion, with increasingly higher deviation both anteriorly and posteriorly.

The specimen shows that the transverse rotation of the plates during early diagenetic compaction may cause lateral expansion of the trunk. The rotation always tends to be directed to the other side than the slope of the sagittal plane, and was therefore toward the left side of the body in the present specimen. During the rotation, the plates tended to push the adjacent cuticle toward the left side; causing a deformation of the shape of the left margin of the body. The cuticle on the right side followed the plates during rotation, and has formed broadly rounded projections on right margin. The trunk diameter after deformation is shown in Table 33.

Table 32. Measurements in ELRC 30012, showing the preserved length of the subdivisions of the body in the present specimen (SL); the reconstructed original length of the subdivisions in ELRC 30060 (OL); and the estimated length of each subdivisions being lost during compaction (△SL) (all figures in mm)

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL	2.7	1.7	2.1	3.3	3.7	3.8	3.6	2.8	1.6	1.7
OL	6.5	2.2	2.2	3.8	3.8	3.8	3.8	3.1	2.5	2.3
△SL	3.8	0.5	0.1	0.5	0.1	0	0.2	0.3	0.9	0.6

All nine pairs of plates are present and the two plates of each pair are widely dislocated, so that both the concave inner face of the left plates and the convex outer face of the right ones were exposed completely by the split of the rock. Each plate is seen to be superimposed by a smaller one and the double plates are interpreted as an indication of double skins in the pre-molt stage. Except for the double plates in the anterior pair which lack dislocation (pl. 3, fig. 2), in most pairs they are seen to be dislocated relative to each other (pl. 2, fig. 2). The specimen shows that the transverse rotation of the plates caused dislocation of the two plates in the double plate pairs, the larger size plate appearing to shift toward the active (left) side of the rotation in the right plates, but toward the positive (right) side in the left ones (see pl. 2, fig. 2). As a consequence, each larger sized plate has

Table 33. Measurements in ELRC 30012, showing the trunk diameter at the plate-bearing points (TWp) and at the midlength between two successive pairs of plates (TWd), in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
TWp	1.9	2.6	3.2	3.6	3.6	3.2	3.0	2.6	2.7
TWd	2.0	2.7	2.6	3.0	2.9	2.8	?	?	?

a broader exposed margin appearing to be restricted either on the dorsal margin of the smaller plate in the right side plates or on the ventral margin in the left ones. The first pair of plates (pl. 3, fig. 2) is the only one in which the outer margin of the larger plate is exposed to form a circular ring beyond the overlying smaller plate. The length and height of the plates in P1 measure 1.20 mm and 0.90 mm in the larger size plate; 1.00 and 0.75 mm in the smaller size plate. This shows that the linear size difference of the plates between two moult stages can be estimated to 20%.

All the right side legs are completely preserved, and several have one or two claws visible at their distal end (Lg1-Lg3, Lg9 and Lg10). The legs in Lg1-Lg3 appear to be more slender and longer than other legs, extended anterolaterally with a length of 4.6 mm in RLg1 and RLg2, and 5.5 mm in RLg3. They have a width of 0.8 mm. Legs RLg4-RLg6 are preserved straight, extended adaxially and ventrally, having a subequal length, 5.0 mm in RLg4, 5.5 mm in RLg5 and 6.0 mm in RLg6, all having a width of 1.2 mm. RLg7-RLg10 are substraight with a gentle anterior curvature in the distal portion of RLg9 and LLg10. They are of the same stout appearance, being 5.0 mm long in RLg7 and RLg9, 4.8 mm in RLg10, all having a width of 1.3 mm. The only legs preserved on the left side are LLg1, LLg5-LLg8. They appear to tilt down at a steeper angle, with a preserved length being much shorter than the original. Their proximal portion is concealed by the laterally expanded part of the body. The position of their juncture with the body wall can be determined by the ventral margin of the left plates. The entire length of these legs, therefore, can be calculated from the fossil and it measures about 3.0 mm in LLg5, 3.0 mm in LLg6, 3.3 mm in LLg7, 4.2 mm in Llg8. The leg LLg1 is extended anteriorly into sediment, having a length of 4.3 mm. All the left side legs are shorter than their right side counterparts (Table 34), suggesting that the left legs are tilted at a steeper angle.

The central canal is well indicated by a fine dark line, present in LLg6-LLg8, RLg4 and RLg7, extending centrally throughout the leg.

The alimentary canal is expressed by a dark band, extending longitudinally in the trunk in a position about two thirds of the transverse width from the right trunk margin. It continues through the entire head, with a width of 0.15 mm. The left-eccentric position of the alimentary canal is suggested to be a consequence of the right-inclined sagittal plane. It indicates that before compaction the vertical distance between the alimentary canal and the ventral margin was relatively longer than between the canal and the dorsal margin.

Table 34. Measurements in ELRC 30012, showing the width (w) and length (1) of the legs of the left (L) and right sides (R), in mm

	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Lg7	Lg8	Lg9	Lg10
R(w)	0.8	0.8	0.8	1.1	1.1	1.1	1.3	1.3	1.3	1.3
R(1)	4.7	4.7	5.2	5.0	5.5	6.0	5.0	5.0	5.0	4.8
L(w)	0.8	-	-	-	-	-	-	1.3	-	-
L(1)	4.3	-	-	-	3.0	3.0	3.3	4.2	-	-

19. ELRC 30051

(Plate 18; figure 1; Text-figure 40; Table 35)

This is a posterior portion of an animal which was buried in a life position; the split of the rock passed along the top surface of the fossil. It has a preserved length of 8 mm, consisting of the posterior 4 subdivisions and 4 pairs of plates. The length of the subdivisions measures 2.5 mm in sdv6, 2.2 mm in sdv7 and 1.9 mm in sdv8 (Table 35). The ventral face, as indicated by the length between the bases of the plates of each pair, is of even width, about 1.2 mm (Table 35).

Annuli are present in areas between two successive pairs of plates. Papillae are seen in the area between plates P6 and P7.

As is evident from the specimen, the plates of each pair were forced by the vertical compaction to reorient into a parallel preservation by a transverse rotation directed toward the left side. The rotation caused a lateral expansion of the left margin appearing to be restricted to the swell regions. Table 35 shows that the trunk width across the swells is 169-193% as long as the height of the plates. In the parallel specimen ELRC 30008 (Table 13 and Table 36), the relation between the diameter of the trunk across the swells and the height of the plates is about 152-159% in sdv6-sdv9. This shows that the lateral expansion caused an increase of the width ranging from 17% to 41%. The trunk width across the depressed areas between swells (see Table 35) is about 1.7 mm and corresponds to 121% of the height of the plate. The figure is very close to that in the parallel preservation (Table 36),

Table 35. Measurements in ELRC 30051, showing the length of the trunk subdivisions (SL); the trunk width across the swells (TWp) and the depressed trunk (TWd); the distance between the ventral margin of the plates of each pair (VW); the PH (height) and PL(length) of a plate of a pair; the relation of the trunk width both across the swells and across the depressed trunk relative to the height of the plates in percent; the relation of the TWd and VW in percent

	sdv6	sdv7	sdv8	sdv9
SL(mm)	2.5	2.2	1.9	1.8
TWp(mm)	2.7	2.7	2.4	2.2
TWd(mm)	1.7	1.7	1.7	?
VW(mm)	1.2	1.2	1.1	0.9
PH(mm)	1.4	1.4	1.4	1.3
PL(mm)	0.9	0.8	0.9	1.2
TWp/PH(%)	193	193	171	169
TWd/PH(%)	121	121	121	?
VW/TWd(%)	71	71	65	

Table 36. Measurements in ELRC 30008, showing the heigth of the plates (PH), the trunk width across the swells (TWp) and the depressed trunk (TWd); and the relation of the trunk width both across the swells and across the depressed trunk relative to the height of the plates in percent

	P6	P7	P8	P9
PH(mm)	2.3	2.3	2.3	2.2
TWp(mm)	3.5	3.5	3.5	3.5
TWd(mm)	2.7	2.7	2.7	-
TWp/PH(%)	152	152	152	159
TWd/PH(%)	117	117	117	-

suggesting that the trunk in the depressions was circular and that the vertical compaction in the present specimen took place without producing a lateral expansion in the depressions which were soft-bodied. As is evident from the distance between the ventral margin of the two plates of each pair, the soft-bodied ventral region is about 1.2 mm wide in sdv6 and sdv7, narrowing posteriorly to 1.1 mm in sdv8 and 0.9 mm in sdv9. The diameter of the trunk as indicated by the TWd is 1.7 mm which is about one-third more than the width of the ventral region.

The alimentary canal is preserved as a dark brown band, about 0.3 mm wide, running longitudinally between the bases of the paired plates at 3/5 of the trunk diameter from the right margin. The eccentric position of the alimentary canal suggests that the sagittal plane of the body sloped down toward the right.

Only the right side legs are present. RLg6 is 3 mm long and 0.5 mm wide, in a gentle curvature with the concave side facing anteriorly. RLg8-RLg10 are extended straight, about 0.7 mm wide and 2.3 mm to 1.7 mm long.

20. ELRC 30049

(Plate 8, figures 1-3; Text-figures 20-21; Table 37) 37)

This specimen is represented by the part (pl. 8, figs. 1-2) and counterpart (pl. 8, fig. 3) of a juvenile, which was buried in life position and compacted dorsally. The entire animal has a preserved length of 22.5 mm. It was buried in a ventrally curved form and its anterior portion was inclined relative to the plane of bedding at an angle of 11° in sdv3, increasing anteriorly to 17° in sdv2, and to 25° in sdv1. The posterior portion, however, tends to incline posteriorly in the sediment at an angle of 11° in sdv5, increasing to 17° in sdv6, and to 18° in sdv7-sdv9. The middle part of the body from P3 to P5 is preserved subparallel to the plane of bedding, lying at the highest stratigraphical position within the specimen, with an elevation of 1 mm above the posterior end and 1.5 mm above the anterior end. If the effect of the compaction is taken into account, the elevation before compation may have been 10 mm or even greater.

Most of the longitudinal sections were altered (shortened) in length due to oblique preservation with the exception of sdv4 which is the only section which was buried parallel to the plane of bedding, thus retaining the original length. Based on the length of sdv4, the original length of the entire animal is estimated to have been 36 mm, with a length of 13.5 mm being lost due to the early diagenetic compaction. The head is curved ventrally and is subparallel-sided, with a broadly rounded front. It measures 2.7 mm in length; its uncompacted length is estinated to have been at least 6 mm. The length of trunk subdivisions is longest in sdv4, shorter both posteriorly and anteriorly.

The sagittal plane of the body is tilted down toward the right side, as indicated by the transverse dislocation of the plates of each pair. The vertical compaction appears to have forced the subvertically-oriented plates of each pair into a horizontal position by means of a transverse rotation with the free dorsal margin moving in the direction opposite to the slope of the sagittal plane and therefore moving to the left side. The ventral margin of the plates played the role of the center of rotation, and is preserved in an unchanged position. The rotation of the plates appears to be directed to the left side; the plates tended to push the adjacent cuticle toward left side, causing formation of the depressions between the two successive pairs of the plates on the right margin of the body. The cuticle on the left side followed the plates during rotation, and has formed broadly rounded projections on left margin. The width of the trunk after deformation and vertical compaction is shown in Table 37.

Because the ventral margin of the plates is preserved in an unchanged position, the distance between the plates of a pair is considered here to be identical to the width of the soft-bodied ventral face of the animal, which measures 1.4 mm at P5 and P6; 1.2 mm at P7; and 10 mm at P8 and P9.

Table 37. Measurements in ELRC30049, showing the length (SL) and the angle of tilt (T°) of the longitudinal subdivisions of the body; the distance between the ventral margin of the plates of each pair (VW); the PH (height) and PL (length) of the plates; the width of the trunk across the plate-bearing points (TWp) and the depressed areas (TWd); and the relation between the PH and TWp in percent; a, anterior; p, posterior

	hd	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	2.7	1.0	1.7	3.0	3.3	3.1	3.0	2.0	1.5	1.5
T°		25°a	18°a	11°a	0°	7°p	17°p	18°p	18°p	18°p
VW(mm)		0.8	0.8	1.1	1.3	1.3	1.3	1.2	1.0	1.0
PH(mm)		1.0	1.1	1.8	1.8	1.9	1.9	1.9	1.8	1.5
PL(mm)		1.2	1.2	1.3	1.3	1.2	1.2	1.2	1.2	1.4
TWp(mm)		1.6	2.1	3.1	3.4	3.5	3.4	3.1	-	-
TWd(mm)		-	-	-	-	-	2.2	-	-	-
TWp/PH(%)		160	191	172	189	184	179	163	-	-
VW/PH(%)		80	67	61	72	68	68	63	56	67

This shows that the width of the soft-bodied ventral area, as indicated by the distance of the ventral margin of the plates of each pair, ranges from 56% to 80% of the PH of the plate.

All nine plate pairs are present. The plates of the EL form (P1), as shown in the counterpart, is in a rounded form, with the PH (height) corresponding to 80% of the PL (length). The figure of PH/PL in most specimens ranges from 55% to 65%. This shows that the PH of P1 in the present specimen is proportionally longer. The P1 and P2 as shown in the counterpart, are dislocated both longitudinally and transversely; the split of the rock was either passing along the inner face of the right plates and outer surface of the left plates or traveling between the overlapped part of the RP1/PL1 and LP1/PR2, thus revealing entirely the inner concave surface of the RP1 and RP2 and the outer convex surface of the LP2. The polygons and tubes are present, but indistinct in the marginal ring-shaped area. They are small, ranging from 0.05-0.02 mm in diameter. The indistinct nature of the preservation indicates that the marginal ring might be buried within the soft tissue. A large area of LP1 was overlapped both with RP1 and RP2, and was removed by the split of the rock.

The duplication structure is seen in all plates. The new and old plates of a duplicated pair usually are dislocated, with the stratigraphically lower one of a duplicated pair having moved in a direction opposite to the slope of the sagittal plane, therefore forwarding the left side in P3 to P5, also anterior in P6 to P9 and posterior in P1 and P2. The height: length of the two of each duplicated pair of the plates measures 1.1:0.9 mm in old, and 1.3:1.1 mm in new one of P2; 1.5:1.1 mm in old, and 1.8:1.3 mm in new one of P3; 1.8:1.0 mm in old, and 2.1:1.2 mm in new one of P6. The linear difference between the old and new one of a duplicated pair shows that the growth rate between two molting stages is about 20% in linear dimension.

The alimentary canal is expressed by a dark band, extending longitudinally in the trunk at a distance from the ventral margin of the right plate equalling about two thirds of the distance between the ventral margins of the plates of a pair. It has a width of 0.3 mm in the trunk and 0.15 mm in the head.

The legs of the left side are largely covered by matrix and only LLg10 was revealed by preparation. Accordingly, most of the legs exposed in the fossil are extending from the right side of the trunk. They are either being bent with the concave side facing anteriorly (RLg9), or extending straight from the trunk (RLg7, RLg6, RLg5, and RLg2). All are vaguely defined and do not show preservation of the claws, with the exception of RLg2 which bears a claw. The length of this leg measures 4 mm.

21. ELRC 30022

(Plate 14, figure 2; Text-figure 31; Table 38)

This specimen represents an individual which was buried in a life position, being subdorsally compacted. The split of the rock passed along the stratigraphically lower surface of the specimen, revealing only a part of the trunk. Most of the fossil was exposed by preparation on the lower surface of the slab. It has a preserved length of 16 mm, representing a nearly complete trunk. The part of trunk posterior to P5 was straight and parallel to the plane of bedding, thus retaining an original length. Based on the length of the parallel preserved trunk subdivisions (Table 38), the animal is estimated to have been 33 mm long. The body anterior to P5 is in a ventral curvature which increases anteriorly and its longitudinal subdivisions were altered in length as an effect of vertical compaction.

The sagittal plane as indicated by the dislocation of the plates of each pair, is tilted down (stratigraphically) to the left side. As is evident from the specimen, the plates of each pair were reoriented into a parallel preservation by a transverse rotation directed to the right side. The rotation caused a lateral expansion of the left margin appearing to be restricted to the swell areas. The width of the trunk across the swells is 187% (in sdv4 and sdv5) and 188% (in sdv6 and sdv7) times the height of the plates. As is evident from the lateral preservation in ELRC 30008 (see Table 13), the width corresponds to 152%-157% of the height of the plates. This shows that the vertical compaction caused an increase of the width across the swells ranging from 30% to 36% of the height of the plates.

Eight pairs of plates are present. The plates of a pair are widely dislocated transversely in P4-P8; the split of the rock was passing along the stratigraphically lower surface of the fossil, thus revealing entirely the concave inner face of the left and convex outer face of the right plates. The trunk tends to tilt anteriorly in its anterior portion (anterior to P4), becoming steeper in the portion of sdv2 and sdv3 where the plates of a pair are widely dislocated in a longitudinal direction, with RP2 appearing to be overlapped by the LP3.

The alimentary canal is represented by a dark, flattened band, about 0.3 mm wide in most parts of the trunk with exception of the posterior part in sdv7 where it appears to be in a lighter, three-dimensional structure. The canal lies subcentrally in sdv6 and sdv7, anteriorly tending to shift toward the left side to a submarginal position.

Five legs are present on the left side; LLg1, LLg3, LLg6-LLg8. The right side legs were, however, mostly removed due to splitting with the exception of RLg1 and RLg5-RLg8 which are partially preserved.

Table 38. Measurements in ELRC 30022, showing the length of the trunk subdivisions (SL); the width of the trunk across the plate-bearing point (TWp); the PH (height) and the PL (length) of plates; and the relation of the PH and the TWp in percent

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.2	1.4	1.6	-	2.9	2.9	3.1	3.0	?
TWp(mm)	1.2	1.3	2.0	2.8	2.8	3	3	>2.6	>2.3
PH(mm)	0.5	1.0	1.5	1.5	1.5	1.6	1.6	1.5	1.2
PL(mm)	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	?
TWp/PH(%)	240	130	133	187	187	188	188	?	?

22. ELRC 30036

(Plate 16; figures 3-4; Text-figures 36-37; Table 39)

The specimen is a juvenile *Microdictyon* which was buried in a life position, being subdorsally compacted. It is represented by part (pl. 16, fig. 4) and counterpart (pl. 16, fig. 3). The animal was buried in a ventral curvature, with the anterior portion lying at a lower stratigraphical level. The specimen shows that the sagittal plane of the animal was tilted to the left side and that the transverse rotation of the plates during early diagenetic compaction has cauased a lateral expansion of the right margin of the trunk, restricted to swell regions. It has a preserved length of 13.5 mm representing a head and nearly complete trunk. The entire length of the animal, as calculated from the length of parallel preservation of the trunk subdivisions, is estimated to have been 20 mm. The head is curved ventrally. The trunk can be subdivided into nine subdivisions with are longest in its middle three subdivisions, shorter both anteriorly and posteriorly (see Table 39). As is evidenced by the longitudinal dislocation of the plates in each pair, the longitudinal axis is curved anteriorly in the head and in sdv1-sdv3 and posteriorly in sdv8 and sdv9, whereas it is parallel to the plane of bedding in the main part of the trunk (see Table 39) in sdv4-sdv7 which, thus, retain their original length.

The width of the trunk across the plate-bearing point measures 1.7 mm in sdv3, sdv4 and sdv8; 2.0 mm in sdv5 and sdv6, 1.9 mm in sdv7, corresponding to 170% to 190% times the height of the plates. In the lateral specimen ELRC 30008 (see Table 13), the width of the TWp in sdv3 to sdv7 ranges from 152% to 158% times the height of the plates. This shows that the vertical compression of the specimen caused an increase of the lateral width corresponding to 18%-38% of the height of the plates.

Table 39. Measurements in ELRC 30036, showing the length of the trunk subdivisions (SL); the angle of tilt in longitudinal direction (T°1); the trunk width across the plate-attached areas (TWp) and the depressed areas (TWd); the distance between the ventral margin of the plates of a pair (VW); the PH (height) and PL (length) of the plates; the relation of the height of plates (PH) with the trunk width across the plate-attached areas (TWp) and the depressed areas (TWd) in percent; a, anterior; p, posterior

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.0	1.1	1.5	1.7	1.8	1.8	1.4	1.1	>0.5
T°1	14°a	5°a	16°a	0°	0°	0°	0°	14°p	-
TWp(mm)	-	-	1.7	1.7	2.0	2.0	1.9	1.7	-
TWd(mm)	-	-	-	1.3	1.3	1.3	1.3	-	-
VW(mm)	-	-	0.7	0.8	0.9	0.9	0.8	0.7	-
PH(mm)	0.4	0.6	1.0	1.0	1.1	1.1	1.0	1.0	0.8
PL(mm)	0.6	0.6	0.7	0.7	0.7	0.7	0.7	0.7	0.8
TWp/PH(%)	-	-	170	170	182	182	190	170	-
TWd/PH(%)	-	-	-	130	118	118	130	-	-
VW/TWd(%)	-	-	-	62	69	69	62	-	-

Table 39 shows that the trunk has an even width of 1.3 mm across the depressed areas in sdv4-sdv7, corresponding to 118-130% times the height of the plate. The figure is very close to that in the parallel preservation (see Table 13). This shows that the trunk was circular in section and the width has not been modified by vertical compaction.

The transverse length between the ventral margin of the plates measures 0.7 mm in sdv3 which increases to 0.9 mm in sdv5 and sdv6, and thus being narrower posteriorly. It corresponds to between 62% and 69% of the trunk width across the depressed areas.

All nine pairs of plates are present. The plates of a pair are dislocated both longitudinally and transversely in P1-P3, and mainly transversely in P4-P9; the split of the rock was either passing along the inner face of the right or outer face of the left plates, thus in the part revealing nearly entirely the concave inner face of the right and convex outer face of the left plates. Duplicated structure is seen in all the plates. The length difference between the newly formed and old one is about 10% to 15%.

The alimentary canal is seen in sdv4 and sdv5 as a dark band (about 0.1 mm wide) extending straight at a position about two thirds to two fifths of the distance between the ventral margin of the plates of a pair from the ventral margin of the left plate.

23. ELRC 30058

(Plate 7, figure 1; Text-figure 18; Table 40)

The specimen is exposed on the stratigraphically lower surface of a slab, representing the anterior portion of an animal buried in a life position, being subdorsally compacted. It has a preserved length of 19 mm, consisting of the head and the anterior 6 subdivisions and 7 pairs of plates. The entire length of the animal is estimated to have been 27 mm, based on the length of the trunk subdivisions. The body is straight but its anterior portion including the anterior two subdivisions and the head, is curved ventrally. The preserved relief indicates that the sagittal plane in the curved part was tilted down to the right side in the sediment. The transverse rotation of the plates during early diagenetic compaction has caused a lateral expansion of the left margin of the trunk restricted to the swell areas. The width of the trunk across the plate-bearing points of P4 and P5, corresponds

Table 40. Measurements in ELRC 30058, showing the length of the head and trunk sections (SL); the angle of tilt in the longitudinal direction (T°1); the trunk width across the swells (TWp) and the depressed areas (TWd); the PH (height) and PL (length) of the plates; the relation of the height of the plates (PH) with the trunk width across the swells (TWp) and the depressed areas (TWd) in percent; a, anterior

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6
SL(mm)	4.5	1.2	1.3	1.8	2.2	2.4	2.3
T°1	16°a	25°a	35°a	14°a	5°a	0°	0°
TWp(mm)	-	-	-	-	2.7	2.8	2.6
TWd(mm)	-	-	-	-	1.7	1.7	-
PH(mm)	-	0.5	0.7	1.2	1.5	1.5	-
PL(mm)	-	1.0	0.7	0.8	0.9	0.9	-
TWp/PH(%)	-	-	-	-	180	187	-
TWd/PH(%)	-	-	-	-	113	113	-

to 180-187% times the height of the plates (Table 40). This shows that the vertical compaction caused an increase of the lateral width corresponding to 1/4 to 1/3 of the height of the plates. The width of the trunk across the depressed areas corresponds to 113% of the height of the plates. This figure is identical to that in the parallel preservation, indicating that the vertical compaction in the soft bodied areas between two successive pairs of plates took place without any detectable lateral expansion.

The longitudinal axis of the body, as indicated by the dislocation of the plates of each pair in the longitudinal direction, is parallel to the plane of bedding in the posterior portion and tilted down in the portion anterior to P4 at a varying angle to the plane of bedding. As an effect of the compaction, the longitudinal sections of the body including the head and trunk subdivisions sdv1 to sdv4 are altered (shortened).

The head is gently curved and subparallel-sided, about 4.5 mm long (measured along the dorsal margin). Seven pairs of plates are present. The split passed the underside of the specimen, usually revealing the concave inner side of the left plates and the convex outer side of the right ones.

The alimentary canal is represented by a brown or dark, flattened band running subcentrally in the trunk between the ventral ends of the two plates of a pair, having a flattened width of 0.3 mm; in the head region it is much narrower and at a submarginal position.

The right side legs in Lg2, Lg4 and Lg5 are present, and are kept straight and parallel to the plane of the bedding in Lg5 or extending ventrolaterally into sediment in Lg2. As an effect of compaction, the length in RLg2 is shortened considerably.

24. ELRC 30039 - ELRC 30041

(Plate 10, figure 1; Text-figure 23; Tables 41-42)

At least three *Microdictyon* individuals occur in the cluster, and are exposed on the stratigraphically upper surface of a slab; they represent animals which were in pre-moult stage and are buried in a life position. ELRC 30041 is the only nearly complete one, having a preserved length of 37 mm, representing a nearly complete trunk which is preserved in an elongated S-shape.

The trunk was buried in a curved form with the longitudinal axis tilted down stratigraphically toward the anterior both in the anterior portion before P4 and in the middle portion of the trunk between P5-P7. As an effect of vertical compaction, they were altered in length whereas the middle portion at P4 and the rear portion behind P8, was parallel to the bedding plane, thus retaining their original length (Table 41). The entire length of the animal, as indicated by the length of the parallel trunk sections, is estimated to have been 47 mm.

When the animal was buried, the plates were subvertically oriented but they tended to tilt down stratigraphically toward the left side in the anterior pairs P1-P5 and toward the other side in the posterior pairs P6-P9. The vertical compaction appears to have acted to force the subvertically oriented plates of each pair to reorient themselves into a horizontal position by means of a transverse

Table 41. Measurements in ELRC 30041, showing the length of the trunk subdivisions (SL); the angle of tilt in the longitudinal direction (T°1); a, anterior

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	3.1	3.3	3.6	2.8-4.0	2.8-4.3	3.8-2.0	4.0-2.0	3.3	-
T°1	16°a	0°	0°	0°	19°a	19°a	19°a	19°a	0°

rotation with the free dorsal margin moving in the direction opposite to the slope of the sagittal plane, thus to the right side in P1-P5 and the left side in P6-P9. The plates of the left side are preserved with their inner concave side up in P1-P5 and down in P6-P9 whereas the concave side of the plates in the right side is facing downward in P1-P5 and upward in P6-P9. The split has thus revealed the inner concave face of RP1-RP5 and LP6-LP9, and the outer convex face of LP1-LP5 and RP6-RP9.

The plates of each pair are widely dislocated, so that both the concave inner face and the convex outer face of the plates are exposed completely during the split of rock. Each plate is seen to be superimposed by a smaller one, and the double plates are interpreted as an indication of a double skin in a pre-molt stage. Except for the double plates in RP1, LP1, LP2, LP7 and LP8 showing no substantial dislocation, they are seen to be dislocated from each other in the remaining plate pairs. Table 42 shows the linear difference between two plates of each double pair which suggests a growth rate between the two moult stages of about 13% to 19% in linear dimension.

As is shown by the evidence of the regularly rounded cutting structure, the plates were very hard. They also appear to have been deformable. When the animal was buried, the plates were vertically extended and the vertical compaction tended to force the vertically oriented plates to be bent to form a smoothly bent, buckled structure in several plates. The vertical compaction also tended to cause a modification of the plates into a considerably flattened shape when the plates were reoriented into a horizontal position.

The alimentary canal is seen as traces of a dark band, extending subcentrally in the interval between P2 to P5. It has a width of 0.3 mm.

Table 42. Measurements in ELRC 30041, showing the height (PH) and length (PL) of the normal-size plates; and the height (PHs) and length (PLs) of the smaller plates

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PH(mm)	1.2	2.0	2.6	3.0	3.0	3.0	3.0	2.8	2.6
PL(mm)	2.2	1.9	1.9	2.0	2.2	2.0	2.0	2.1	2.9
PHs(mm)	-	1.7	2.3	2.6	2.6	2.7	2.7	-	2.2
PLs(mm)	-	1.6	1.6	1.8	1.9	1.7	1.7	-	2.6

ELRC 30039 and ELRC 30040 also occur in the cluster, lying posterior and anterior to ELRC 30041, respectively. Both are only partially exposed on the surface.

25. ELRC 30033 - ELRC 30034

(Plate 13, figure 1)

This specimen shows a co-occurrence of two *Microdictyon* juveniles which were buried in life position, being subdorsally compacted. The two fossils were revealed by preparation from the underside of a slab. ELRC 30033 (the left one) has a preserved length of 6 mm, represented by 5 pairs of plates. The length of the trunk subdivisions measures 0.7 mm in sdv2, 1.1 mm in sdv3, 1.4 mm in sdv4, and 1.4 mm in sdv5. The entire length of the animal, as indicated by the length of the subdivisions, is estimated to have been 17 mm. The alimentary canal is represented by a vague trace of a dark band, extending subcentrally in the trunk.

ELRC 30034 (the right one) has a preserved length of 5.2 mm, consisting of 4 pairs of plates and 3 subdivisions. The length of the trunk subdivisions ranges from 1.5 to 1.7 mm. The entire length of the animal is estimated to have been 19 mm, based on the length of the subdivisions. The alimentary canal is expressed by a dark band, extending longitudinally between the ventral margin of the plates of a pair at a subcentral position.

26. ELRC 30031

(Plate 15, figure 1; Text-figure 32; Table 43)

This is nearly complete specimen of a juvenile which was buried in life position, being subdorsally compacted. The sagittal plane is tilted down toward the left side; the longitudinal axis is nearly straight and parallel to the plane of bedding but in the anterior portion, including the head and the anterior two subdivisions, the axis is curved ventrally. The preserved length of the animal measures 13 mm whereas the original length, as indicated by the length of the trunk subdivisions (see Table 43), is

Table 43. Measurements in ELRC 30031, showing the length of the head and trunk subdivisions (SL) in mm

	head	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	2.7	0.4	0.7	1.2	1.5	1.5	1.4	1.4	1.3	1.2?

estimated to have been 17 mm.

Papillae are present in the areas between the two successive pairs of plates in sdv3, sdv4, sdv6 and sdv7. They are closely distributed and expressed as dark, positive dots about 0.05 mm across.

The specimen is exposed on the top surface of a slab. As is evident from the specimen, the plates of each pair were forced by the vertical compaction to reorient into a parallel preservation by a transverse rotation directed to the right side, revealing the concave inner face of the right plates. The left-side plates are in convex shape; in the posterior two plates the split passed over the outermost surface of the plates, with preservation of the nodular structure.

The alimentary canal is expressed by a vague, dark band, extending subcentrally but within the left side. The legs exposed in the fossil are poorly preserved, extending from the left side of the trunk.

27. ELRC 30011

(Plate 17, figure 1; Text-figure 38; Table 44)

This is the anterior portion of an adult *Microdictyon* which was buried obliquely, with the sagittal plane tilted down toward the left side at an angle calculated to 7° in sdv5 and sdv4; 23°-20° in sdv3 and sdv2; 15° in the head and sdv1 (see Table 44). The animal was curved ventrally; the longitudinal axis, therefore, has a varying angle of tilt to the plane of bedding in its different parts and as an effect of compaction the length of the trunk sections is altered. The specimen preserves a length of 29 mm, representing a complete head region, the anterior 4 trunk subdivisions and 5 pairs of plates. Based on the length of the preserved part, the original length of the entire animal is estimated to have been 66 mm.

Annuli are present in areas between two successive pairs of plates.

The head, as measured along its dorsal margin, is 8.3mm long. It is gently curved and subparallel-sided, tapering anteriorly in width from 2.2 mm to 2.0 mm, with a broadly rounded front. All the legs in the specimen are either entirely lost (LLg1) or incompletely preserved (LLg2-LLg4), or partially (RLg1 and RLg5) or entirely covered by matrix or the body.

The alimentary canal is preserved as a trace of a dark band extending longitudinally at a submarginal position.

Table 44. Measurements in ELRC 30011, showing the length of the head and trunk subdivisions (SL); angle of tilt both in transverse (T°t) and in longitudinal direction (T°1); v, ventral, p, posterior

	head	sdv1	sdv2	sdv3	sdv4	sdv5
SL(mm)	8.3	3.4	3.9	5.0	5.6	-
T°t	15°v	15°v	20°v	23°v	7°v	7°v
T°1	0°	0°	7°p	7°p	23°p	23°p

28. ELRC 30042

(Plate 20, figure 1; Text-figure 44; Tables 45-46)

This is a *Microdictyon* in a pre-molt stage which was buried in a life position, adjacent to a dorsal-side down buried *Naraoia* (see Text-fig. 44). The split of the rock passed to a stratigraphically lower surface at *Microdictyon* and the intermedidate area but adjacent to the dorsal surface of *Naraoia,* separating both *Microdictyon* and *Naraoia* into two parts. The major part of the *Microdictyon* is exposed from the lower surface of the slab which is assigned as part and illustrated here (pl. 20, fig. 1). It has a preserved length of 34 mm representing a nearly complete trunk. The entire length of the animal, as indicated by the length of the trunk sections, is estimated to have been 47 mm. It is curved ventrally with the sagittal plane tilted down (stratigraphically) to the left side. The longitudinal axis, as indicated by evidence of the longitudinal dislocation of the plates of a pair, is parallel to the plane of bedding in most parts except for the posterior three subdivisions which are tilted posteriorly at an angle of tilt of about 18°.

The soft parts in the body are only partially preserved; disposition of the plates shows that the trunk subdivisions are longest in sdv4 and sdv5, shorter both anteriorly and posteriorly (Table 45).

All nine pairs of plates are present. The plates of a pair are dislocated mainly transversely in P4-P6 and both transversely and longitudinally in P1-P3

Table 45. Measurements in ELRC 30042, showing the length of the body sections in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	2.3	2.3	3.4	4.0	4.2	3.5	3.0	3.0	2.7

and P7-P9. The plates of each pair are widely dislocated. They appear to be made of very tough matter, their rigid girdle having acted as a wedge to force the opposite plate apart when the two plates of a pair were pressed upon each other under the forces of vertical compaction. The cutting edge around the plate is usually seen as a smoothly rounded shape in the right-side plates. The split of the rock went through the outer face of the outlying part of the right side plates and the inner surface of the opposite ones. It usually traveled between the two plates of a pair in the overlapping part of the plate. The cutting edge is not present in P9 in which the split is along the entire surface of RP9 and the inner face of the outlying part of LP9.

A duplicated structure, with smaller plates superimposed on the normal-sized ones, is present in all the plates. This duplicated occurrence is interpreted as an indication of double skins of the pre-molt stage. The linear size difference of the plates between two molt stages ranges from 15% to 23% (see Table 46).

Table 46. Measurements (in mm) in ELRC 30042, showing the difference in height (PH) and length (PL) of each pair of duplicated plates that carry smaller ones (with the suffix -s) superimposed on the normal ones (with the suffix -n)

	P1	P2	P3	P4	P5	P6	P7	P8	P9
PHs	0.90	-	-	2.0	2.0	2.1	2.1	2.0	2.0
PLs	1.45	-	-	1.3	1.4	1.25	1.15	1.8	-
PHn	1.10	-	-	2.3	2.3	2.4	2.45	2.35	2.3
PLn	1.75	1.5	1.6	1.6	1.7	1.5	1.45	2.1	2.1

DESCRIPTIONS OF SPECIMENS DIRECTLY ATTACHING TO *ELDONIA*

29. CLUSTERED OCCURRENCE (NIGP 108294-108296; ELRC 30062-30066)

(Plate 3, figure 1; plate 4, Text-figures 13-14; Tables 47-48)

This is a unique specimen showing a cluster of *Microdictyon* and inarticulate brachiopods which were buried together with *Eldonia*. The *Eldonia* is expressed as a vaguely defined, dark brown, flattened film. The radial canals are visible only in a few areas. The entire animal is estimated to have been about 70 mm in diameter. The split of the rock passed the flattened *Eldonia* fossil, revealing a cluster both of *Microdictyon* and inarticulate brachiopods attaching to the *Eldonia*. At least seven *Microdictyon* individuals are observed to attach to the *Eldonia*. Three of them were illustrated by Chen *et al.* in 1989 and provided with catalogue numbers: NIGP 108294 (Chen *et al.,* 1989, pl. 3, fig. 6-1), NIGP 108295 (fig. 6-2) and NIGP 108296 (fig. 6-3).

NIGP 108294 is a subdorsally preserved juvenile which is represented both by part (pl. 3, fig 1; M3 in Text-fig. 13) and counterpart (pl. 4; M3 in Text-fig. 14). It has a preserved length of 12 mm, representing a complete trunk. It was buried in a life position, dorsally compacted. The dislocation of the plates of a pair shows that the trunk appears to be largely straight and parallel to the plane of bedding except for its anterior part which is curved ventrally. The sagittal plane is tilted ventrally toward the right side of the animal. The length of the trunk subdivisions measures 0.7 mm in sdv1, 1.0 mm in sdv2, and 1.5 mm both in sdv3 and sdv4. The complete length of the animal, as indicated by the length of the trunk subdivisions, is estimated to have been 17 mm. Except for P6 and P7 which are lost by the splitting, all the plates are present; exposed with the concave inner face of the left plates and convex outer face of the right ones.

NIGP 108295 (see M1 both in Text-figs. 13 and 14) is a nearly complete specimen of a juvenile which was buried in life position, being subdorsally compacted. It is represented by part (pl. 3, fig. 1) and counterpart (pl. 4). The sagittal plane of the specimen is tilted ventrally toward the left side. It has an extended length of about 12 mm representing a complete trunk with nine subdivisions and all nine plate pairs. The entire length of the animal, based on the length of the trunk subdivisions (Table 47), is estimated to have been 17 mm. Only the legs of the left side are present; they show a length of 3 mm in LLg3 whereas in LLg6 and LLg7 they are shorter, about 2.3 mm long.

Table 47. Measurements in NIGP 108295, showing the length of the trunk subdivisions (SL) in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.0	1.1	1.2	1.5	1.5	1.4	1.4	1.3	?

NIGP 108296 (see M2 in Text-figs. 13-14) is a juvenile which was buried in life position, being subdorsally compacted. It is represented by part (pl. 3, fig. 1) and counterpart (pl. 4), having a preserved length of 7 mm, representing a complete trunk with all nine pairs of plates. The length of the subdivisions measures 0.6 mm in sdvl, 0.8 mm in sdv2, 1.1 mm in sdv3-sdv5, 1.0 mm in sdv6, and 0.9 mm in sdv7 and sdv8. The entire length of the animal is estimated to have been 13 mm.

Five additional *Microdictyon* individuals have now been revealed by preparation, and provided with the following numbers: ELRC 30062-30066. ELRC 30062 (see M4 of Text-fig. 14) represents a juvenile, being subdorsally compacted. It is exposed on the lower surface of the overlying slab (pl. 4), being straight, with a preserved length of 9 mm representing a main portion of the trunk with seven pairs of plates. The sagittal plane appears to be tilted down stratigraphically toward left side. The length of the trunk subdivisions measures 0.8 mm in sdv2, 1.2 mm in sdv3, 1.5 mm in sdv4, 1.2 mm in sdv5, 1.3 mm both in sdv6 and sdv7. The entire length of the animal is estimated to have been 17 mm.

ELRC 30063 (see M5 in Text-fig. 14) is only partially exposed and the major part of the specimen is concealed by matrix. It has an exposed length of 3.7 mm from the lower surface of the overlying slab, representing only a subdivision with the length of 2.4 mm. The dislocation of the plates of a pair suggests that the animal was buried obliquely. The entire length of the animal is estimated to have been about 27 mm.

ELRC 30064 (see M6 in Text-figs. 13 and 14) is an adult being subventrally compacted. It is represented by part (pl. 4; M6 in Text-fig. 14) and counterpart (pl. 3, fig. 1; M6 in Text-fig. 13), having a preserved length of 22 mm representing a nearly complete trunk with all nine plate pairs. The plates of each pair are widely dislocated transversely. The sagittal plane, as indicated by the transverse dislocation of the plates of a pair, is tilted down (stratigraphically) to the right side. The body is straight in most parts of the trunk, except for its anterior and posterior part where the longitudinal axis is curved ventrally in sediment (see Table 48). The entire length of the animal is estimated to have been 39 mm. The split of the rock largely went along the stratigraphically lower surface of the fossil and the plates are mainly exposed on the lower surface

Table 48. Measurements in ELRC 30064, showing the length of the trunk subdivisions (SL) in mm; the angle of tilt of the trunk subdivisions in longitudinal direction (T°1); a, anterior; p, posterior

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.2	2.0	2.8	3.1	3.5	3.3	2.8	2.0	-
T°1	25°a	0°	0°	0°	0°	0°	7°p	10°p	12°p

of the overlying slab revealing a concave inner face of the left side plates and a convex outer face of the right side ones. This indicates that the animal was buried up-side down and the plates were subvertically oriented with dorsal side down. The vertical compaction appears to have forced the subvertically oriented plates of each pair to reorient into a horizontal position by means of a transverse rotation with the free ventral margin moving in a direction opposite to the tilt of the sagittal plane.

ELRC 30065 (M7) is represented by part (pl.4; Text-fig. 14) and counterpart (pl. 3, fig. 1; Text-fig. 13). It is dorsally compacted, having a preserved length of 5 mm representing four trunk subdivisions with length ranging from 1.2 mm to 1.8mm in each. The entire length of the animal is estimated to have been 20 mm.

Besides the cluster occurrence of seven *Microdictyon* on the same *Eldonia,* which is interpreted as a floating object, there are five inarticulate brachiopods belonging to a single species recently described as *Lingulella chengjiangensis* (Jin *et al.,* 1993) (ELRC 65078-ELRC 65082) and one *Cardiodictyon* (ELRC 31005) (see pl. 4 and Text-fig. 14). All the brachiopods appear to be of the same size, with preservation of the pedicles which are kept in straight or twisted form. The pedicles, as indicated from one nearly complete specimen, have a length of at least 34 mm. The *Cardiodictyon* has a preserved length of 7.5 mm, representing 16 segments of the trunk.

30. ELRC 30046

(Plate 14, figure 1; Text-figure 30; Table 49)

The *Microdictyon* described and illustrated here was a juvenile and buried in a direct attachment to an *Eldonia.* The *Eldonia* was buried upside down, with a diameter of 62 mm. The split of the rock passed parallel through the disc separating the *Eldonia* into two parts. The *Microdictyon* fossil is mainly exposed on the lower surface of the overlying slab, attaching to the outer part of the *Eldonia* disc. It is curved ventrally and has a preserved length of 13.5 mm, representing a major portion of the trunk. The transverse dislocation of the plates of a pair suggests that the animal was buried with its sagittal plane tilted down (stratigraphically) toward the dorsal side. The entire length of the animal, as indicated from the length of the trunk subdivisions (Table 49), is estimated to have been 21 mm.

Only the right legs in Lg5 and Lg6 are present; they are gently curved with the concave side facing anteriorly. The alimentary canal is represented by a dark brown, flattened band extending subventrally through the trunk.

Table 49. Measurements in ELRC 30046, showing the length of the trunk subdivisions (SL) in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8
SL(mm)	1.3?	1.5	1.7	1.9	1.8	1.6	1.3	-

31. ELRC 30045
(Plate 1, figure 2; Table 50)

This specimen is a juvenile *Microdictyon* which was buried in a life position, attached to the disc of an *Eldonia*. The *Microdictyon* is straight, with a preserved length of 15 mm representing a nearly complete trunk with all nine plate pairs. The sagittal plane is tilted down toward the left side. The entire length of the *Microdictyon,* as indicated by the length of the trunk subdivisions (see Table 50), is estimated to have been 23mm.

Table 50. Measuremenets in ELRC 30045, showing the length of the trunk subdivisions (SL) in mm

	sdv1	sdv2	sdv3	sdv4	sdv5	sdv6	sdv7	sdv8	sdv9
SL(mm)	1.2	1.3	2.0	2.1	2.1	2.1	2.0	1.8	-

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REFERENCES

Abele, L. G., Kim, W. and Felgenhauer, B. E., 1989. Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea. *Molecular Biology and Evolution, 6:* 685-691.

Ballard, J. W. O., Olsen, G. J., Faith, D. P., Odgers, W. A., Rowell, D. M. and Atkinson, P. W., 1992. Evidence from 12S ribosomal RNA sequences that onychophorans are modified arthropods. *Science, 258:* 1345-1348.

Bengtson, S., 1991. Oddballs from the Cambrian start to get even. *Nature, 351:* 184-185.

Bengtson, S., Conway Morris, S., Cooper, B. J., Jell, P. A. and Runnegar, B. N., 1990. Early Cambrian fossils from South Australia. *Memoir of the Association of Australasian Palaeontologists, 9:* 1-364.

Bengtson, S., Matthews, S. C. and Missarzhevsky, V. V., 1986. The Cambrian netlike fossil *Microdictyon.* In A. Hoffman and M. H. Nitecki (eds.), *Problematic Fossil Taxa,* 97-115. Oxford University Press, New. York.

Budd, G., 1993. A Cambrian gilled lobopod from Greenland. *Nature, 364:* 709-711.

Chen Junyuan, Bergström, J., Lindström, M. and Hou Xianguang, 1991. The Chengjiang fauna-oldest soft-bodied fauna on Earth. *National Geographic Research & Exploration, 7(1):* 8-19.

Chen Junyuan, Edgecombe, G. D., Ramsköld, L. and Zhou Guiqing (in press). Head segmentation in *Fuxianhuia:* Implications for arthropod evolution. *Science.*

Chen Junyuan and Erdtmann, B. D., 1991. Lower Cambrian fossil Lagerstätte from Chengjiang, Yunnan, China: Insights for reconstructing early metazoan life. In Simonetta, A. M. and Conway Morris, S. (eds.): *The early evolution of Metazoa and the significance of problematic taxa,* 57-76. Cambridge University Press, Cambridge.

Chen Junyuan, Hou Xianguang and Lu Haozhi, 1989a. Early Cambrian netted scale-bearing worm-like sea animal. *Acta Palaeontologica Sinica, 28:* 1-16 (In Chinese, with English summary).

Chen Junyuan, Hou Xianguang and Lu Haozhi, 1989b. Early Cambrian hock glass-like rare sea animal *Dinomischus* (Entoprocta) and its ecological features. *Acta Palaeontologica Sinica 28:*58-71 (In Chinese, with English summary).

Chen Junyuan, Hou Xianguang and Lu Haozhi, 1989c. Lower Cambrian leptomitids (Demospongea), Chengjiang, Yunnan. *Acta Palaeontologica Sinica 28:* 17-31 (In Chinese, with English summary).

Chen Junyuan, Hou Xianguang and Li Guoxiang, 1990. New Lower Cambrian demosponges *Quadrolaminella* gen. nov. from Chengjiang, Yunnan. *Acta Palaeontologica Sinica 29:* 402-414 (In Chinese, with English summary).

Chen Junyuan, Ramsköld, L. and Zhou Guiqing, 1994. Evidence for monophyly and arthropod affinity of Cambrian giant predators. *Science, 264:* 1304-1308.

Chen Junyuan, Zhou Guiqing and Ramsköld, L., 1995. A new Early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China. *Transactions of the Royal Society of Edinburgh, Earth Sciences, 86* (in press).

Conway Morris, S., 1977. A new metazoan from the Cambrian Burgess Shale of British Columbia. *Palaeontology, 20:* 623-640.

Conway Morris, S., 1986. The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). *Palaeontology, 29:* 423-467.

Conway Morris, S., 1990a. Late Precambrian and Cambrian soft-bodied faunas. *Annual Review of Earth and Planetary Sciences, 18:* 101-122.

Conway Morris, S., 1990b. Late Precambrian-Early Cambrian metazoan diversification. In Briggs. D. E. G. and Crowther, P. R. (eds.), *Palaeobiology, a synthesis,* 30-36. Blackwell Scientific Publications, Oxford.

Conway Morris, S., 1992. Burgess Shale-type faunas in the context of the "Cambrian explosion": a review. *Journal of the Geological Society, 149:* 631-636.

Conway Morris, S., 1993. The fossil record and the early evolution of the Metazoa. *Nature, 361:* 219-225.

Dean, D., Rankin, J. S. and Hoffmann, E., 1964. A note on the survival of polychaetes and amphipods in stored jars of sediments. *Journal of Paleontology, 38:* 608-609.

Delle Cave, L. and Simonetta, A. M., 1975. Notes on the morphology and taxonomic position of *Aysheaia* (Onychophora?) and of *Skania* (undeterminated phylum). *Monitore Zoologico Italiano, N. S., 9:* 67-81.

Dzik, J. and Krumbiegel, G., 1989. The oldest 'onychophoran' *Xenusion:* a link connecting phyla. *Lethaia, 22:* 169-181.

Fortey, R. A. and Thomas, R. H., 1993. The case of the velvet worm. *Nature, 361:* 205-206.

Gee, H., 1992. Something completely different. *Nature, 358:* 456-457.

Ghiselin, M. T., 1993. Review: The Early Evolution of Metazoa and the Significance of Problematic Taxa. *Systematic Biology 42:* 106-107.

Gould, S. J., 1992. The reversal of *Hallucigenia. Natural History 1/92:* 12-20.

Gould, S. J., 1993. *Eight Little Piggies-Reflections in Natural History,* 479pp. W. W. Norton & Co., New York.

Hao Yichun and Shu Degan, 1987. The oldest well-preserved Phaeodaria (Radiolaria) from southern Shaanxi. *Geoscience, 1:* 301-310 (In Chinese, with English summary).

Harris, T. M., 1974. *Williamsoniella lignieri:* its pollen, and the comparison of spherical pollen grains. *Palaeontology, 17:* 125-148.

Hinz, I., 1987. The Lower Cambrian microfauna of Comley and Rushton, Shropshire, England. *Palaeontographica, A, 198:* 41-100.

Ho, C. S., 1942. The phosphate deposits of Tungshan, Chengjiang, Yunnan. *Geological Bulletin, 35:* 97-106.

Hou Xianguang, 1987a. Oldest Cambrian bradoriids from eastern Yunnan. *Stratigraphy and Palaeontology of Systematic Boundaries in China, Precambrian-Cambrian Boundary, vol. 1,* 537-545. Nanjing University Publishing House.

Hou Xianguang, 1987b. Two new arthropods from Lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica, 26:* 236-256 (In Chinese, with English summary).

Hou Xianguang, 1987c. Three new large arthropods from Lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica, 26:* 272-285 (In Chinese, with English summary).

Hou Xianguang, 1987d. Early Cambrian large bivalved arthropods from Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica, 26:* 286-298 (In Chinese, with English summary).

Hou Xianguang and Bergström, J., 1991. The arthropods of the Lower Cambrian Chengjiang fauna, with relationships and evolutionary significance. In Simonetta, A. M. and Conway Morris, S. (eds.): *The early evolution of Metazoa and the significance of problematic taxa,* 179-187. Cambridge University Press, Cambridge.

Hou Xianguang and Bergström, J., 1994. Palaeoscolecid worms may be nematomorphs rather than annelids. *Lethaia, 27:* 11-17.

Hou Xianguang and Chen Junyuan, 1989. Early Cambrian arthropod-annelid intermediate animal, *Luolishania* gen. nov., from Chengjiang, Yunnan, *Acta Palaeontologica Sinica, 28:* 208-213 (In Chinese, with English summary).

Hou Xianguang, Ramsköld, L. and Bergström, J. 1991. Composition and preservation of the Chengjiang fauna - a Lower Cambrian soft-bodied biota. *Zoologica Scripta, 20:* 359-411.

Hutchinson, G. E., 1930. Restudy of some Burgess Shale fossils. *Proceedings of the United States National Museum, 78*(11): 1-24.

Jin Yugan, Hou Xianguang, and Wang Huayu, 1993. Lower Cambrian pediculate lingulids from Yunnan, China. *Journal of Paleontology, 67:* 788-798.

Kukalová-Peck, J., 1991. Fossil history and the evolution of hexapod structures. In Naumann, I. D. and CSIRO (eds.): *The insects of Australia, 2nd ed.,* 141-179. Melbourne University Press, Melbourne.

Kukalová-Peck, J., 1992. The "Uniramia" do not exist: the ground plan of the Pterygota as revealed by Permian Diaphanopterodea from Russia (Insecta: Paleodictyopteroidea). *Canadian Journal of Zoology, 70:* 236-255.

Levinton, J. S., 1992. The Big Bang of animal evolution. *Scientific American, November, 1992:* 52-59.

Liang Qizhang, Fang Wu, and Van der Voo, R., 1990. Further study on palaeomagnetism of the Precambrian-Cambrian boundary candidate stratotype section at Meishucun, Yunnan, China. *Acta Geologica Sinica, 60:* 264-274.

Lu, Y. H. and Zhu, Z. L., 1981. Summary of the Cambrian biostratigraphy of China. *Short Papers for the 2nd International Symposium on the Cambrian System. U.S. Geological Survey, Open File Report 81-743:* 121-122.

Luo Huilin, Jiang Zhiwen, Wu Xiche, Song Xueliang, and Ouyang Lin, 1982. *The Sinian-Cambrian Boundary in eastern Yunnan, China,* 1-265. People's Publishing House of Yunnan Province.

Manton, S. M., 1972. The evolution of arthropod locomotory mechanisms. Part 10, Locomotory habits, morphology and evolution of hexapod classes. *Journal of the Linnean Society London, Zoology, 51:* 203-400.

Manton, S. M., 1977. *The Arthropoda: Habits, Functional morphology and Evolution,* 1-527. Oxford University Press, Oxford.

McMenamin, M. A. S. and McMenamin, D. L. S., 1990. *The Emergence of Animals-The Cambrian Breakthrough.* x+217pp. Columbia University Press, New York.

Missarzhevsky, V. V. and Mambetov, A. M., 1981. Stratigrafiya i fauna pogranichnykh sloev kembriya i dokembriya Malogo Karatau. [Stratigraphy and fauna of the Precambrian-Cambrian boundary beds of Malyj Karatau]. *Trudy Geologicheskogo Instituta AN SSR, 326:* 1-92 (In Russian).

Pompeckj, J. F., 1927. Ein neues Zeugnis uralten Lebens. *Palaeontologische Zeitschrift, 9:* 287-313.

Ramsköld, L., 1992a. The second leg row of *Hallucigenia* discovered. *Lethaia, 25:* 221-224.

Ramsköld, L., 1992b. Homologies in Cambrian Onychophora. *Lethaia, 25:* 443-460.

Ramsköld, L. and Hou Xianguang, 1991. New early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature, 351:* 225-228.

Ruhberg, H. and Institut für den Wissenschaftlichen Film, 1985. Morphologie und Lebensweise von Onychophoren. *Publikationen zu wissenschaftlichen Filmen (Institut für den Wissenschaftlichen Film, Göttingen), Sektion Biologie, Ser. 17,* No. 1 (for Film C 1554), 19 pp.

Seilacher, A., 1991. Commentary on "The Chengjiang fauna-oldest soft-bodied fauna on Earth". *National Geographic Research & Exploration, 7(2):* 239.

Shear, W. A., 1992. End of the 'Uniramia' taxon, *Nature, 359:* 477-478.

Shu Degan and Chen Ling, 1988. Discovery of Early Cambrian Radiolaria and its significance. *Scientia Sinica ser. B, 8:* 881-886 (In Chinese).

Simonetta, A. M., 1976. Remarks on the origin of the Arthropoda. *Atti della Società Toscana di Scienze Naturali, Memorie, Ser. B, 82*(for 1975): 112-134.

Sun Weiguo and Hou Xianguang, 1987a. Early Cambrian Medusae from Chengjiang, Yunnan, China. *Acta Palaeontologica Sinica, 26:* 257-271.

Sun Weiguo and Hou Xianguang, 1987b. Early Cambrian worms from Chengjiang, Yunnan, China: *Maotianshania* gen. nov. *Acta Palaeontologica Sinica, 26:* 299-305.

Tiegs, O. W., 1947. The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus. Quarterly Journal of Microscopic Science, 82:* 165-336.

Tiegs, O. W. and Manton, S. M., 1958. The evolution of the Arthropoda. *Biological Reviews, 33:* 255-337.

Tong Haowen, 1989. A preliminary study on the *Microdictyon* from the Lower Cambrian of Zhenba, South Shaanxi. *Acta Micropalaeontologica Sinica, 6:* 97-101.

Walcott, C. D., 1911. Cambrian Geology and Paleontology, II, 5. Middle Cambrian annelids. *Smithsonian Miscellaneous Collections, 57:* 109-144.

Walcott, C. D., 1931. Addenda to descriptions of Burgess Shale fossils (with explanatory notes by C. E. Resser). *Smithsonian Miscellaneous Collections, 85(3):* 1-46.

Walossek, D. and Müller, K. J., 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences, 85:* 1-37.

Walton, J., 1936. On the factors which influence the external form of fossil plants: with descriptions of foliage of some species of the Palaeozoic equisetalean genus *Annularia* Sternberg. *Philosophical Transactions of the Royal Society of London, B 226:* 219-237.

Wheeler, W. C., Cartwright, P. and Hayashi, C. Y., 1993. Arthropod phylogeny: a combined approach. *Cladistics 9:* 1-39.

Whittington, H. B., 1978. The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, B 284:* 165-197.

Wingstrand, K. G., 1972. Comparative spermatology of a pentastomid, *Raillietiella hemidactyli,* and a branchiuran crustacean, *Argulus foliaceus,* with a discussion of pentastomid relationships. *Kongelige danske Videnskabernes Selskab Biologiske Skrifter, 19:* 1-72.

Zhang Wentang, 1987. Early Cambrian Chengjiang fauna and its trilobites. *Acta Palaeontologica Sinica, 26:* 223-235 (In Chinese, with English summary).

Zhang Wentang and Hou Xianguang, 1985. Preliminary notes on the occurrence of the unusual trilobite *Naraoia* in Asia. *Acta Palaeontologica Sinica, 24:* 591-595 (In Chinese, with English summary).

寒武紀葉足動物*Microdictyon sinicum*

陳均遠　周桂琴　拉姆雪爾達

摘　要

微網蟲是寒武紀早期動物群的重要成員，與現生有爪類的造型十分相似。微網蟲早就以其造型十分奇特的骨片出現於科學文獻。一直到1989年，由於微網蟲完整化石的發現，人們才非常意外地認識到這些骨片竟然是長在毛蟲狀生物身軀的兩側。自1989年以來，又陸續發現了70多塊完好的化石標本，這些發現爲深入了解微網蟲解剖學的特徵提供了可能。根據同源比較分析，本文對微網蟲前後定向重新進行了解釋。據新的解釋，微網蟲具有細長的頭部，口在頭的終端；身軀次圓柱狀，表面具橫紋，有10對帶爪的腿；腿的表面具橫紋。軀幹兩側嵌有9對堅硬的骨片，這些骨片有時呈雙疊狀，新形成的骨片比未脫落的骨片約大13-20%。小型微網蟲常與*Eldonia*(已絕滅浮游生物)在一起，表明微網蟲幼年期營假浮游生活方式。微網蟲與負有盛名的*Hallucigenia*，以及其他寒武紀葉足類構成具有親密演化關係的共源類群，至於這一類群與現生有爪類的演化關係，在本文暫作懸案。

關鍵詞：微網蟲，葉足類，寒武紀大爆炸，澄江，演化。

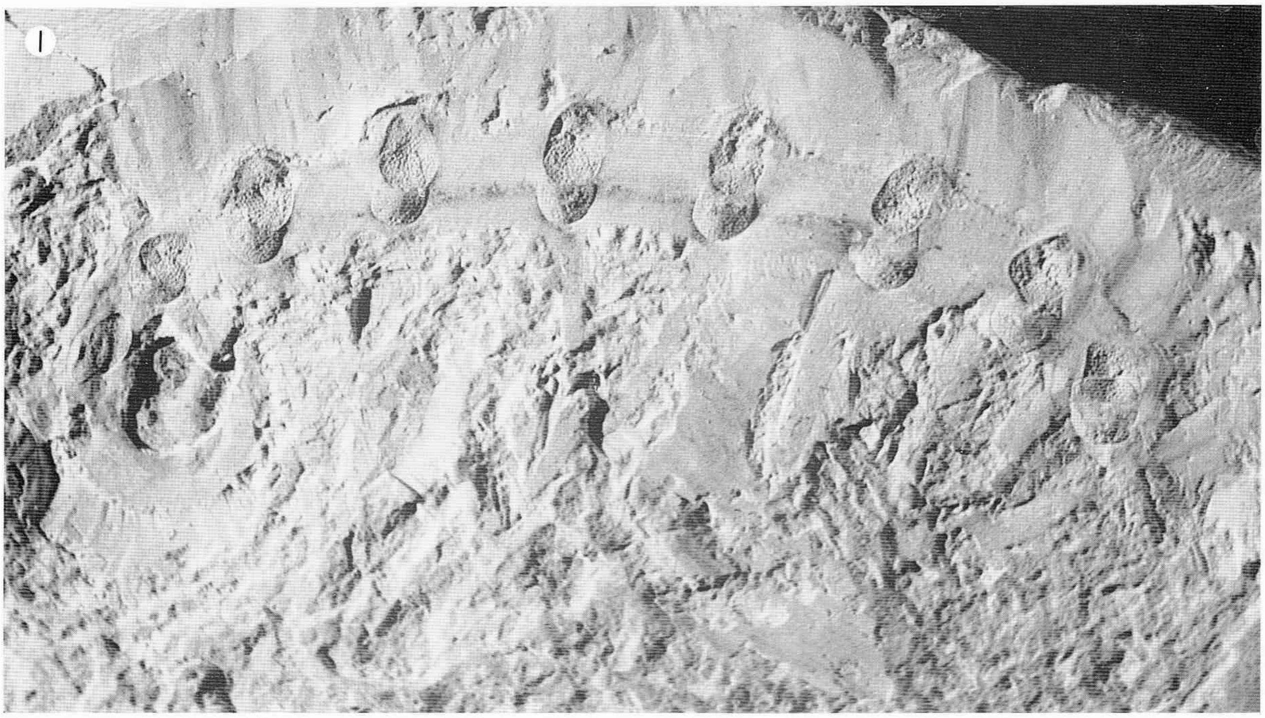
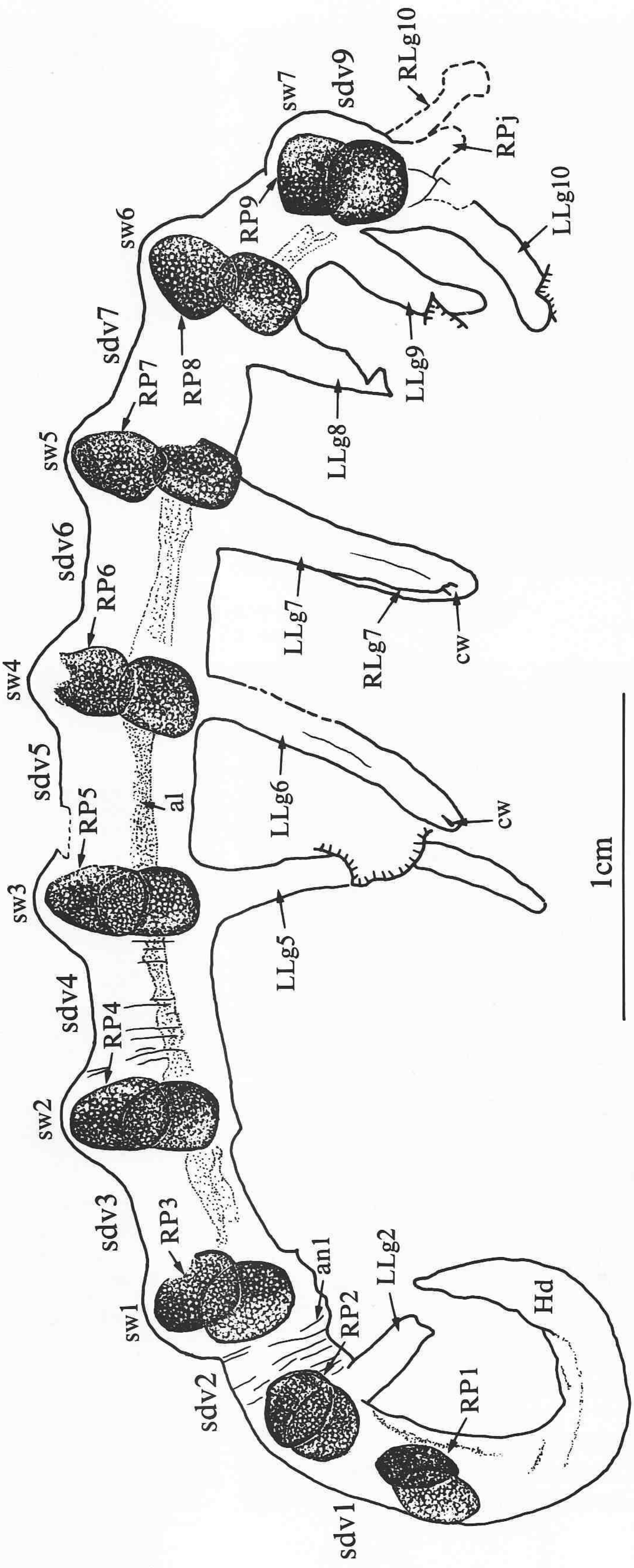


Plate 1

Figure 1. Holotype, NIGP108286, M2, X3.4, parallel specimen, NW; see text-figure 11.

Figure 2. ELRC 30045, MQA, X7, showing a *Microdictyon* in direct contact with an *Eldonia;* NE.



Text-figure 11

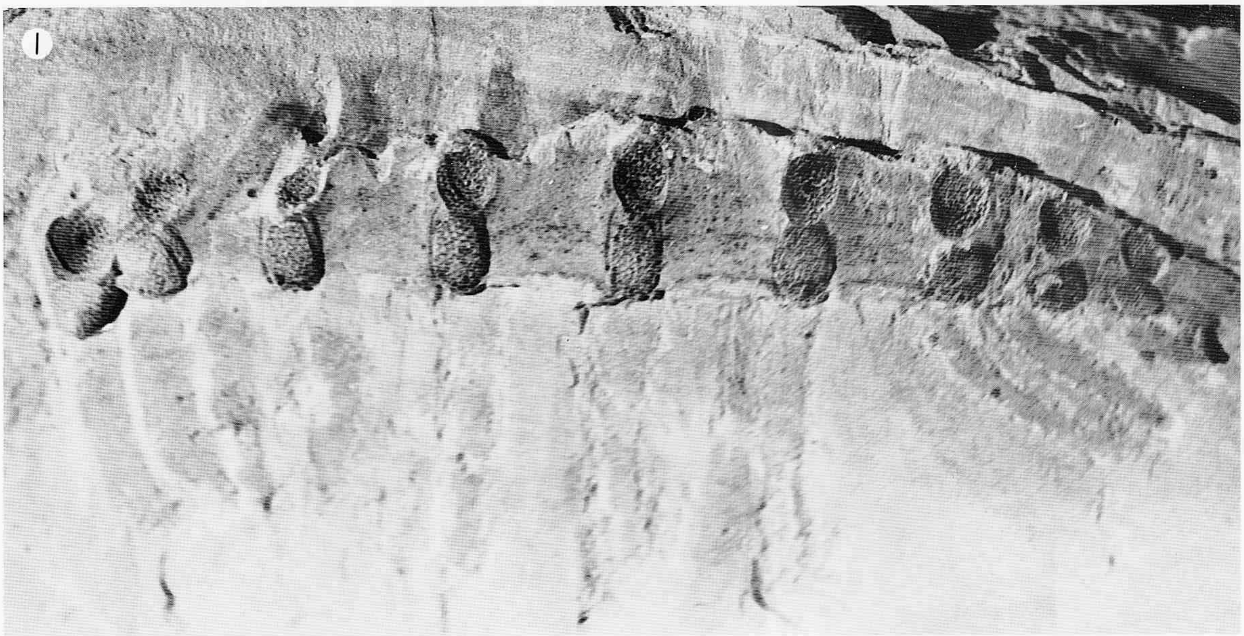
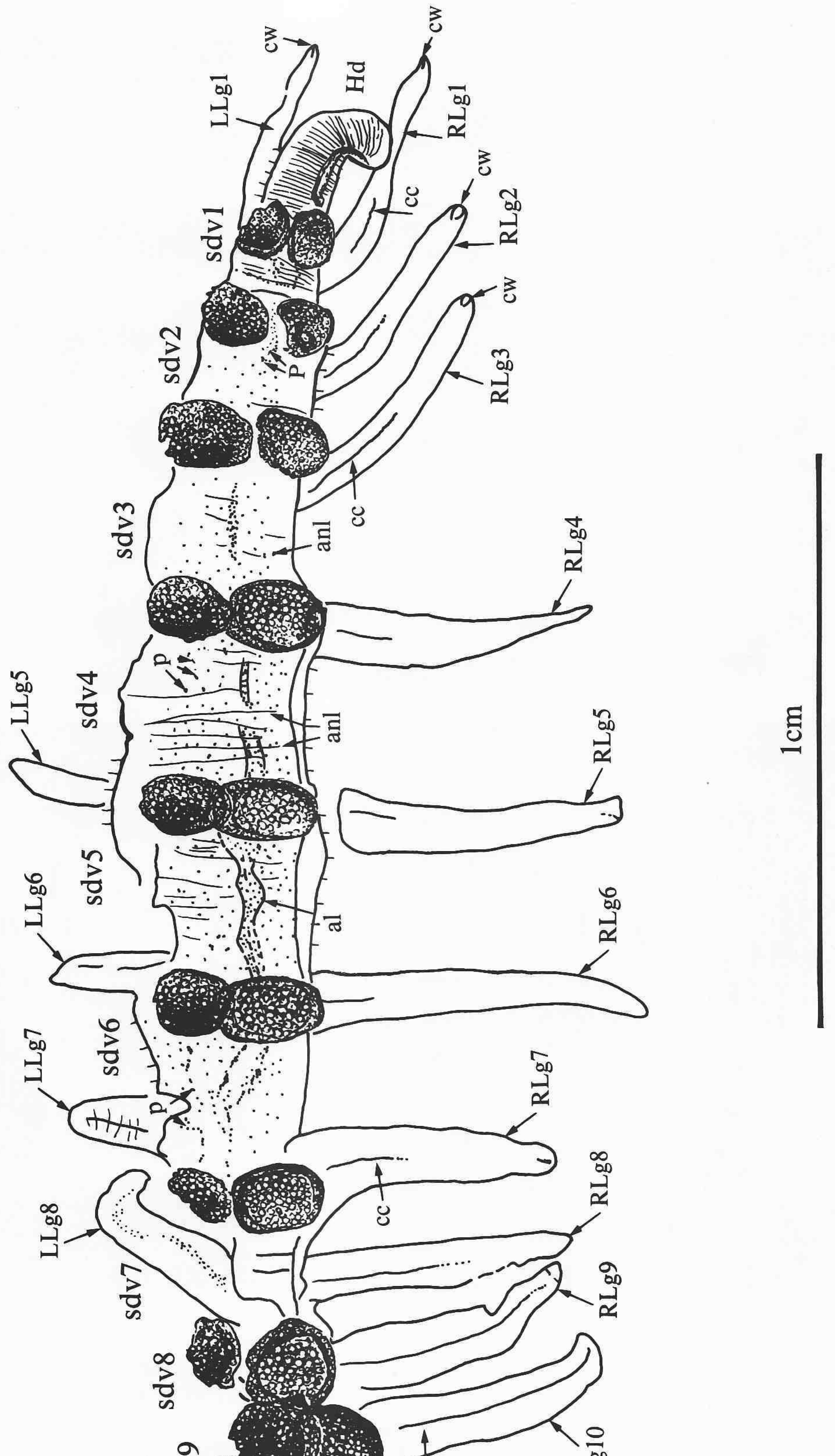


Plate 2

Figure 1. ELRC 30012, MN5, X6, subdorsal specimen, WNW, see text-figure 12.

Figure 2. Enlargement of the posterior portion of ELRC 30012, MN5, X9, showing papillae and double plates, WNW; see text-figure 12.

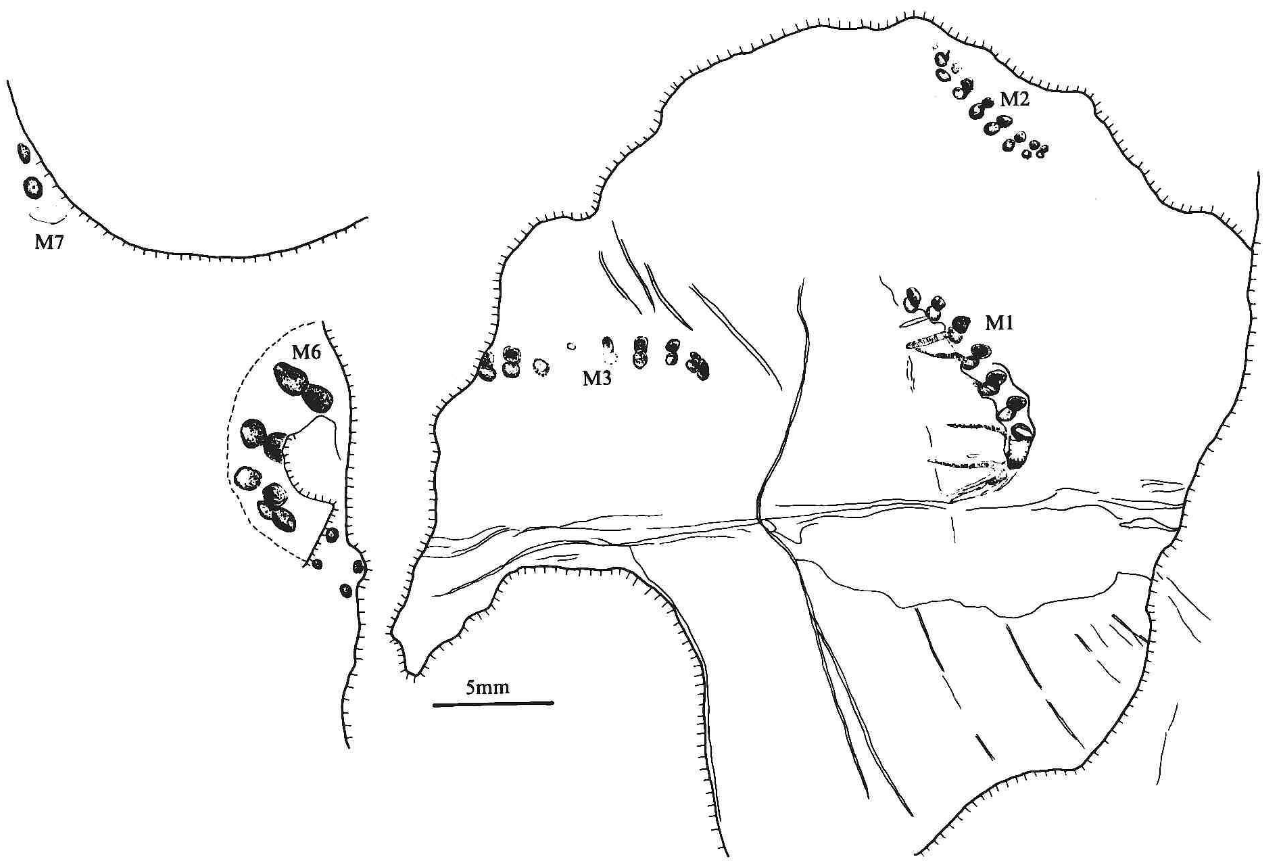


Text-figure 12

Plate 3

Figure 1. Counterpart of an *Eldonia* (pl. 4) and five of the seven associated *Microdictyon:* part of M1 (NIGP 108295); M2 (NIGP 108296); M3 (NIGP 108294); and M7 (ELRC 30065); and counterpart of M6 (ELRC 30064); M2, X3, ENE; see text-figure 13.

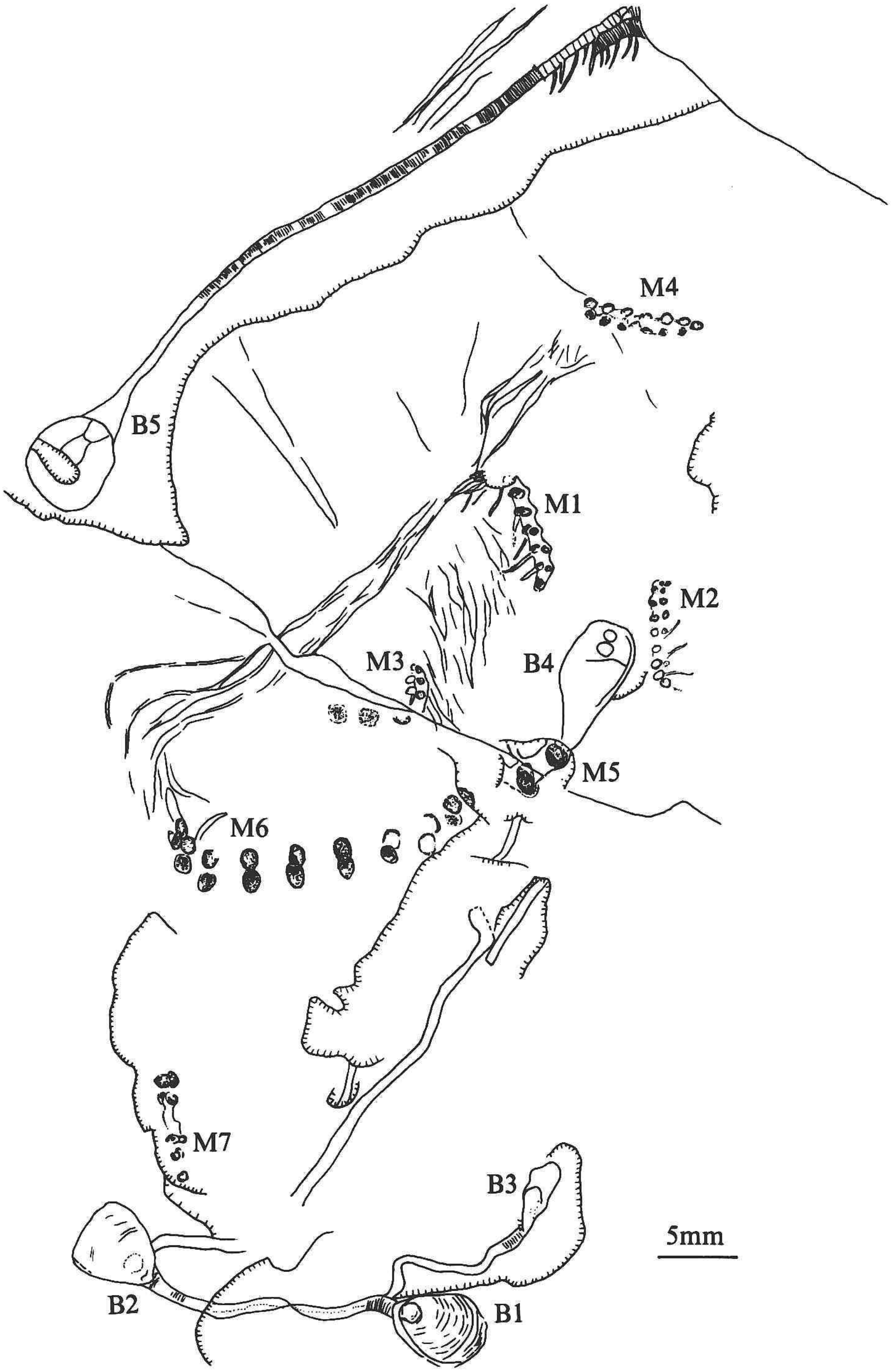
Figure 2. Anterior portion of ELRC 30012, MN5, X11, showing curved head tilted down into sediment to the right side, WNW; see text-figure 12.



Text-figure 13

Plate 4

Part of an *Eldonia* (pl. 3, fig. 1) and seven associated *Microdictyon:* counterpart of M1 (NIPG 108295); M2 (NIGP108296); and M3 (NIGP 108294); part of M4 (ELRC 30062), M5 (ELRC 30063), M6 (ELRC 30064); and counterpart of M7 (ELRC 30065); five inarticulate brachiopods preserved with pedicle B1-B5 which are provided with the numbers ELRC 65078-65082 and a *Cardiodictyon,* C (ELRC 31005), M2, X3, NW; see text-figure 14.



Text-figure 14

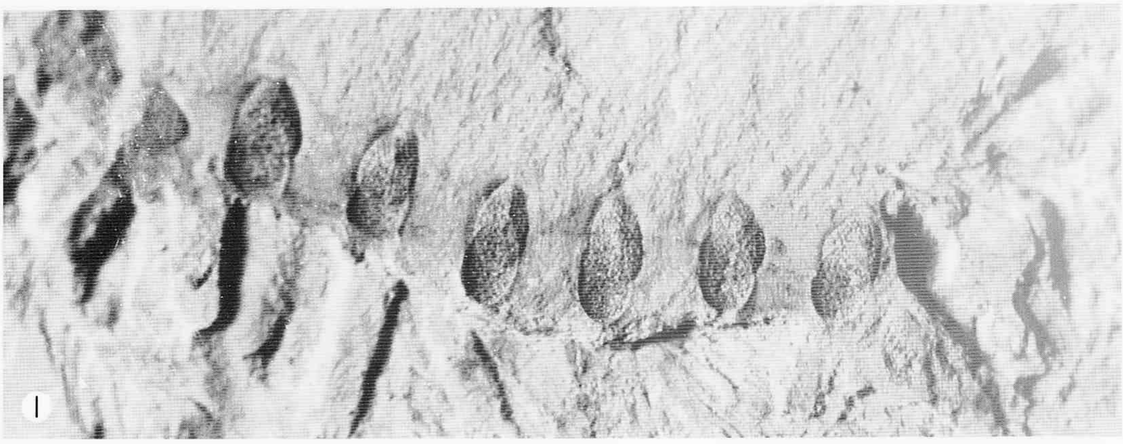
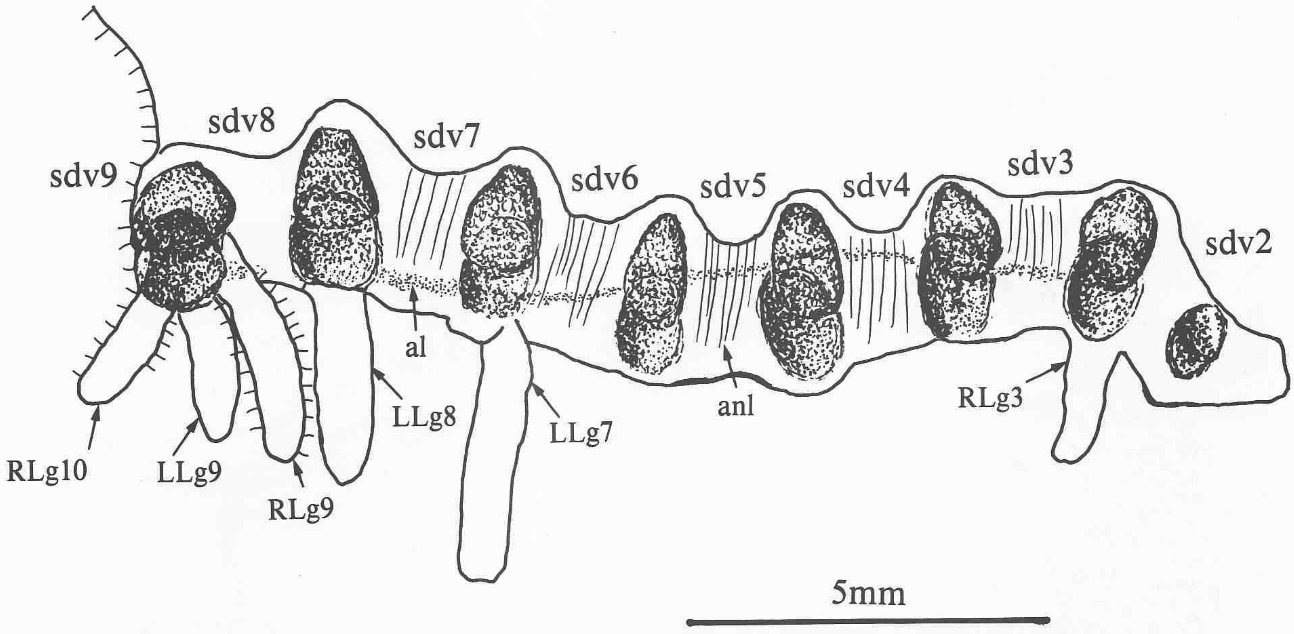


Plate 5

Figure 1. NIGP 108289, M2, X7.5, obliquely compacted specimen, WNW; see text-figure 15.

Figure 2. A *Microdictyon* (ELRC 30060) co-occurring with an *Eldonia* (ELRC 01059), MN5, X1.6, NE.



Text-figure 15

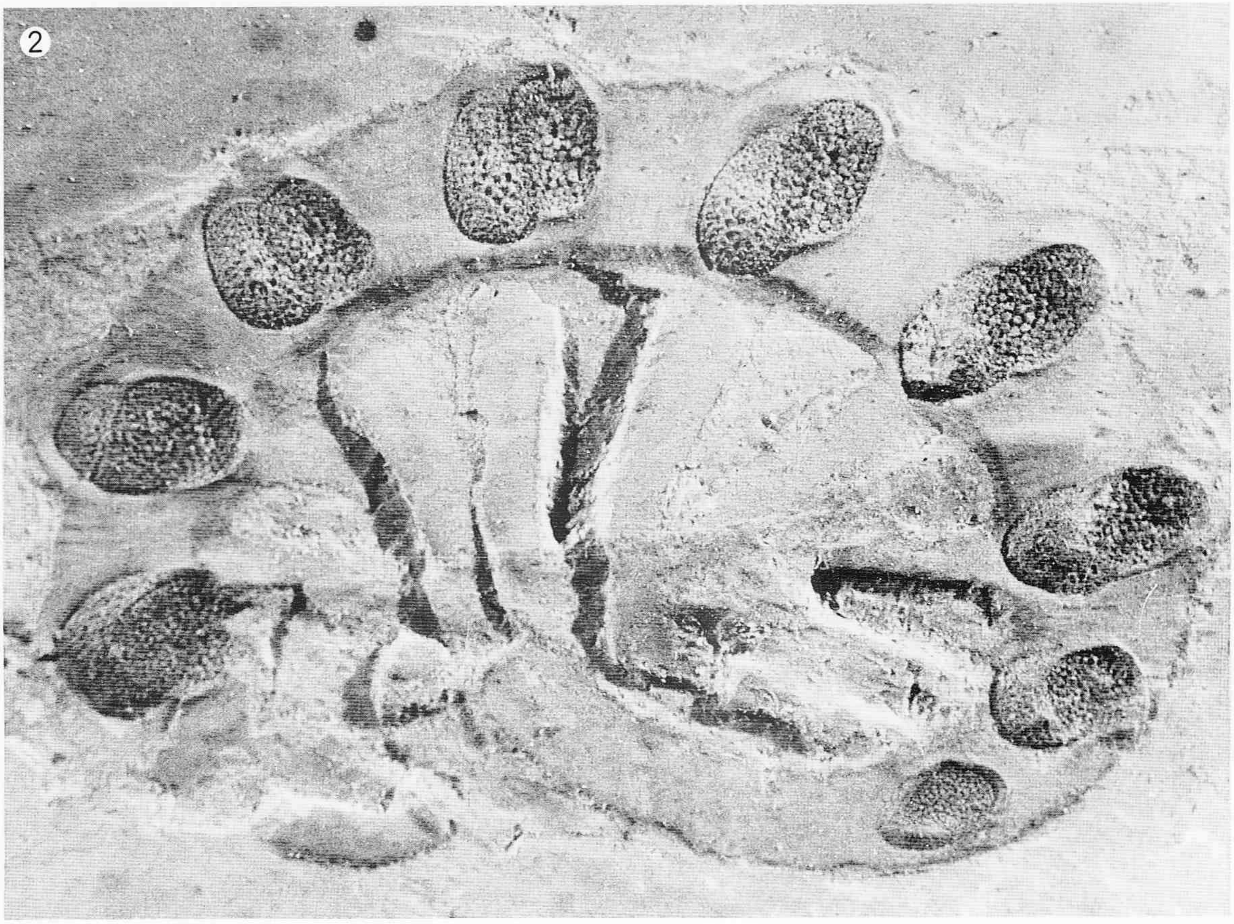
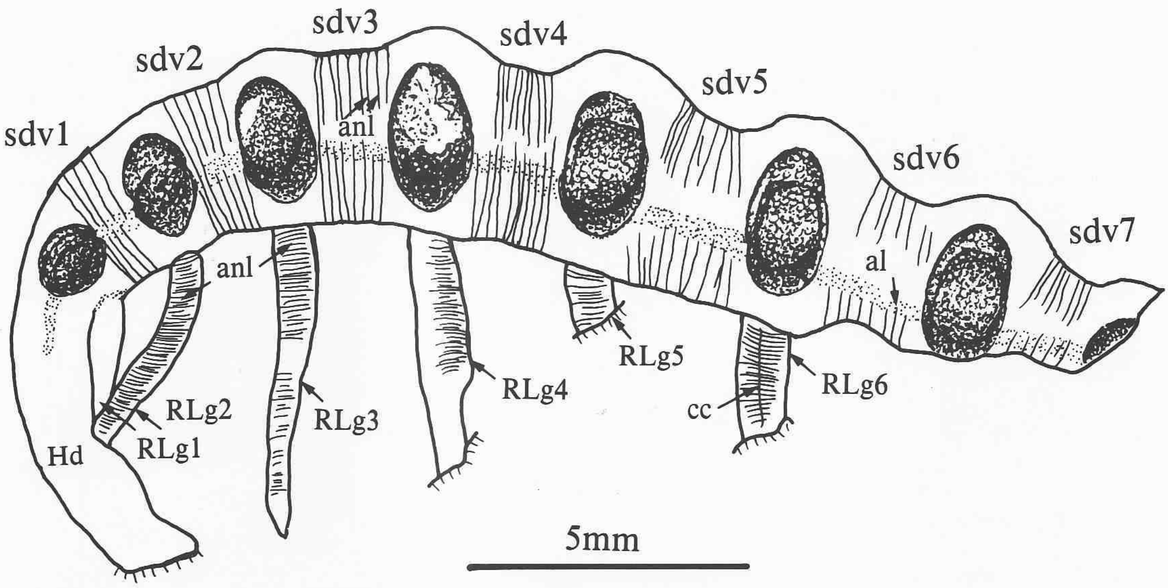
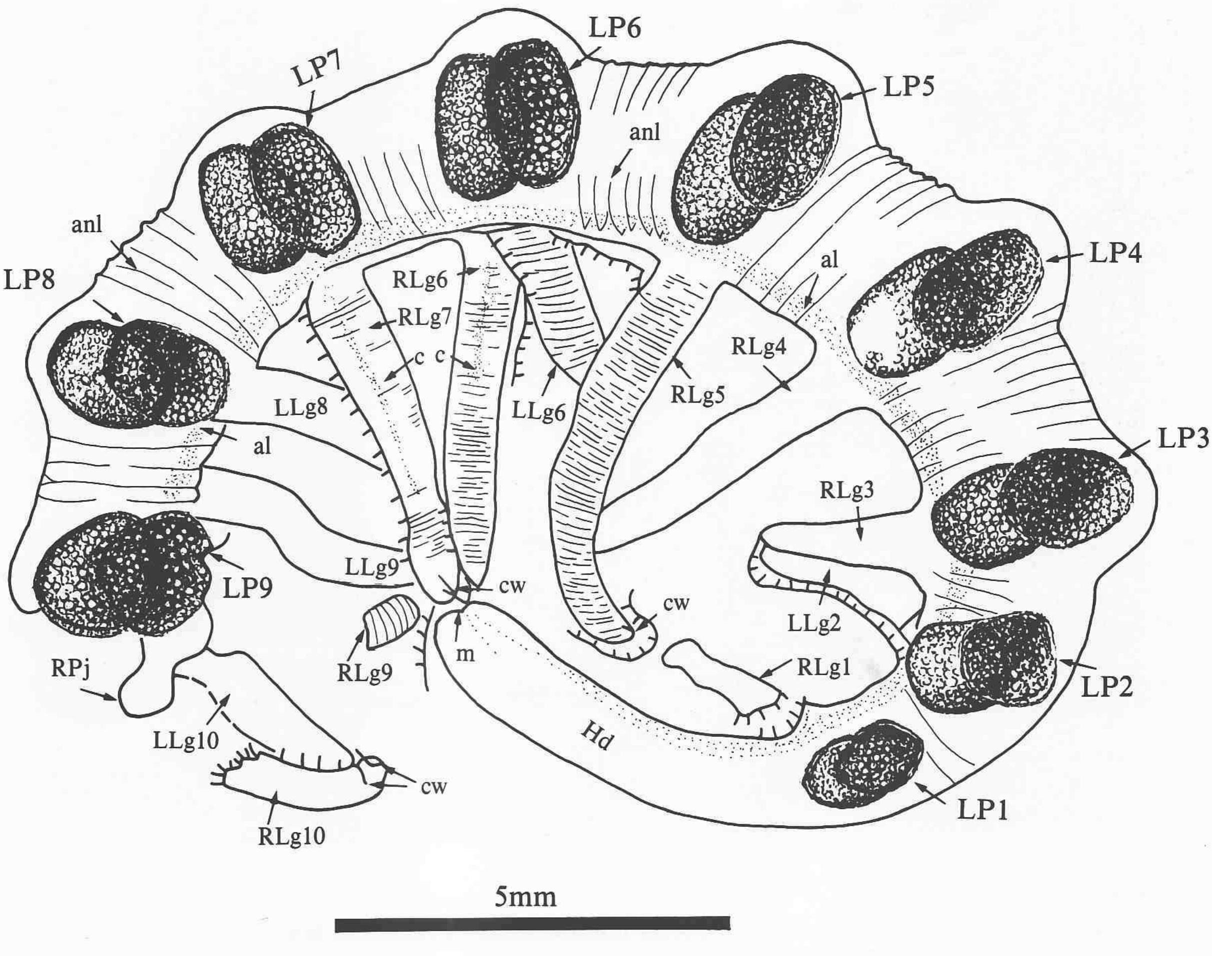


Plate 6
Figure 1. Part of ELRC 30007, X6.5, lateral compaction, NW; see text-figure 16.
Figure 2. ELRC 30060, MN5, X10.7, sublateral compaction, NE; text-figure 17.



Text-figure 16

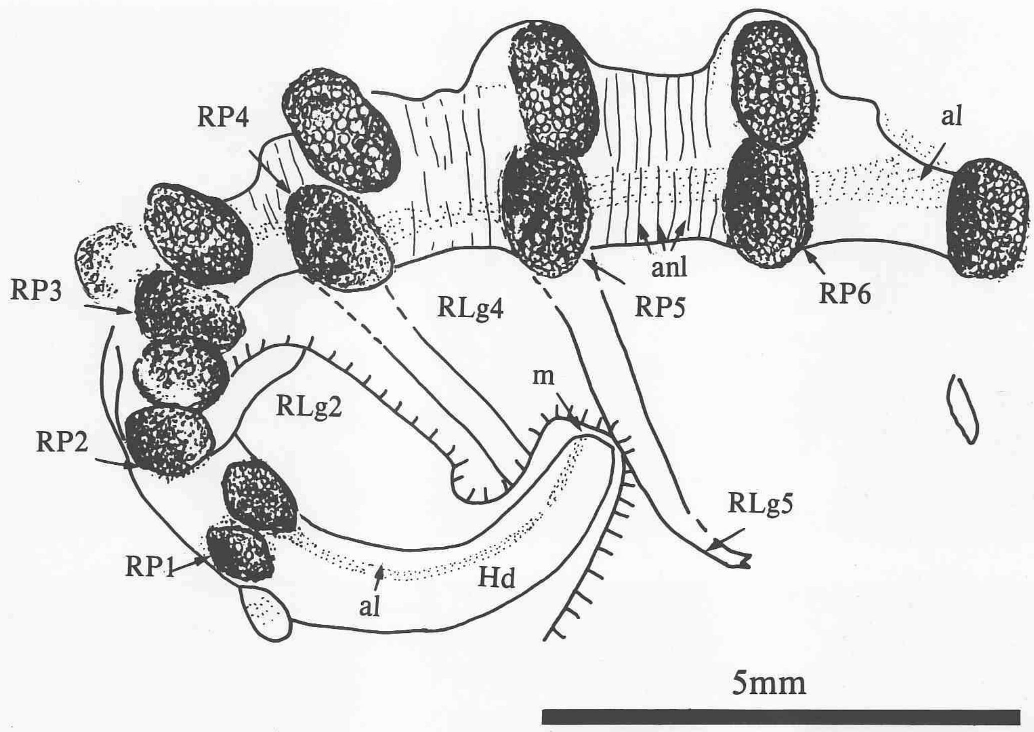


Text-figure 17

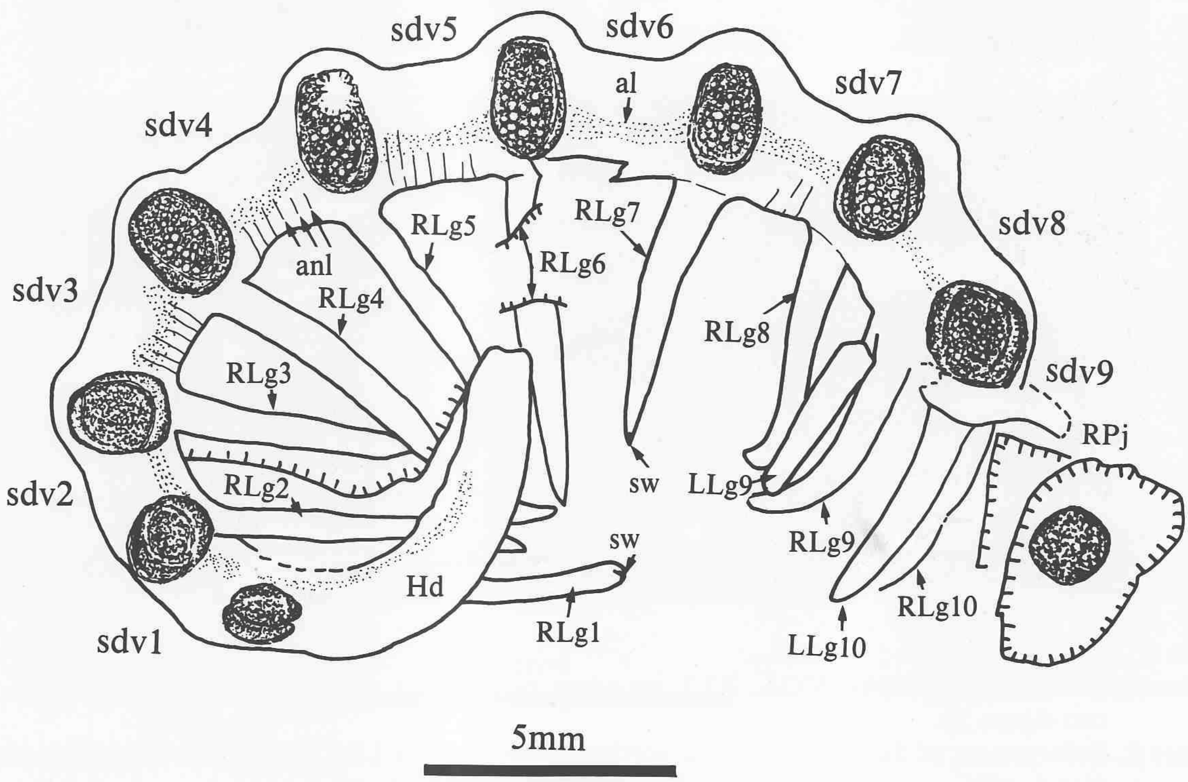
Plate 7

Figure 1. ELRC 30058, X13.5, subdorsal compaction, WNW; see text-figure 18.

Figure 2. NIGP 108287a, X7, lateral specimen, WNW; see text-figure 19.



Text-figure 18



Text-figure 19

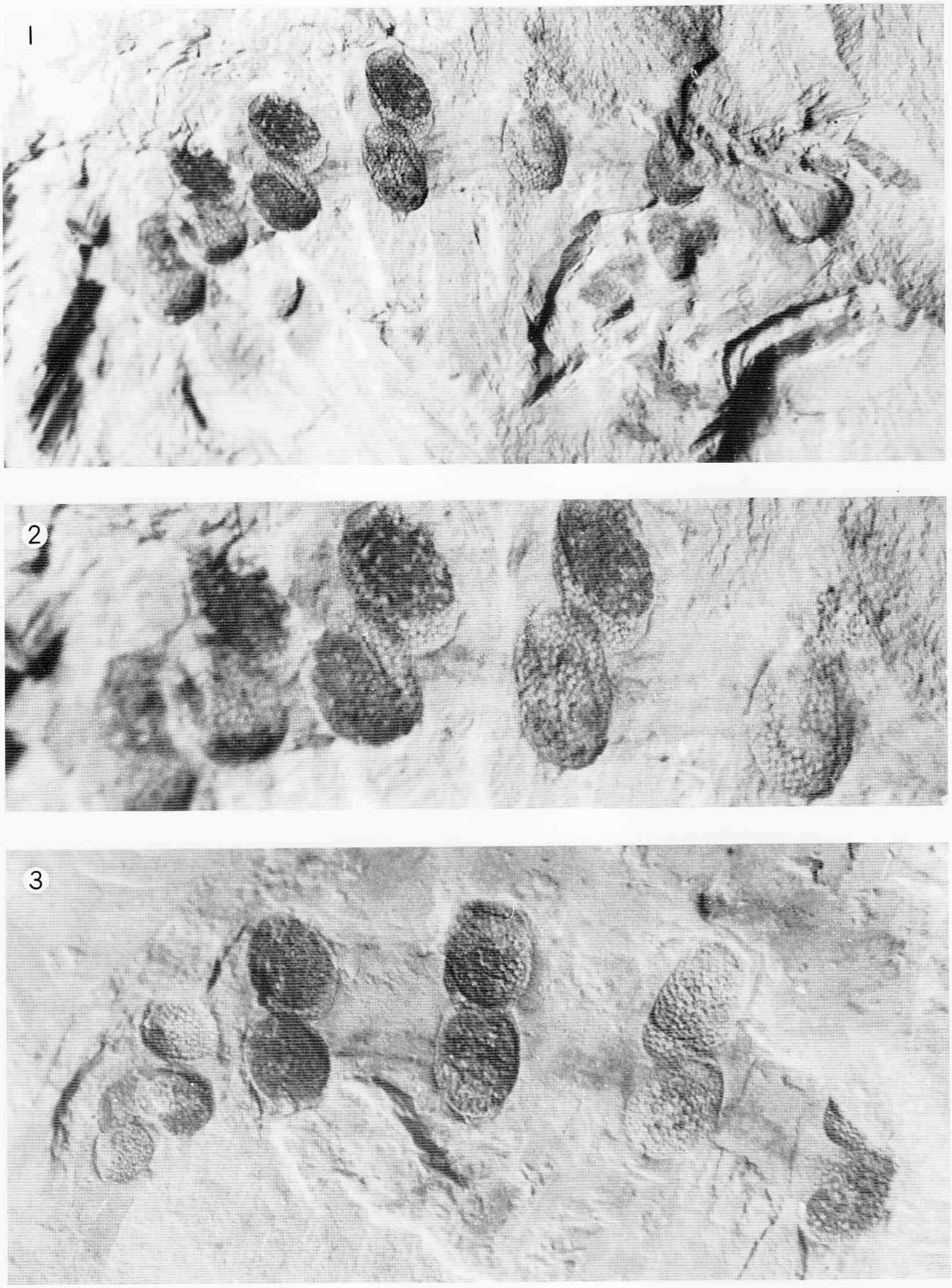
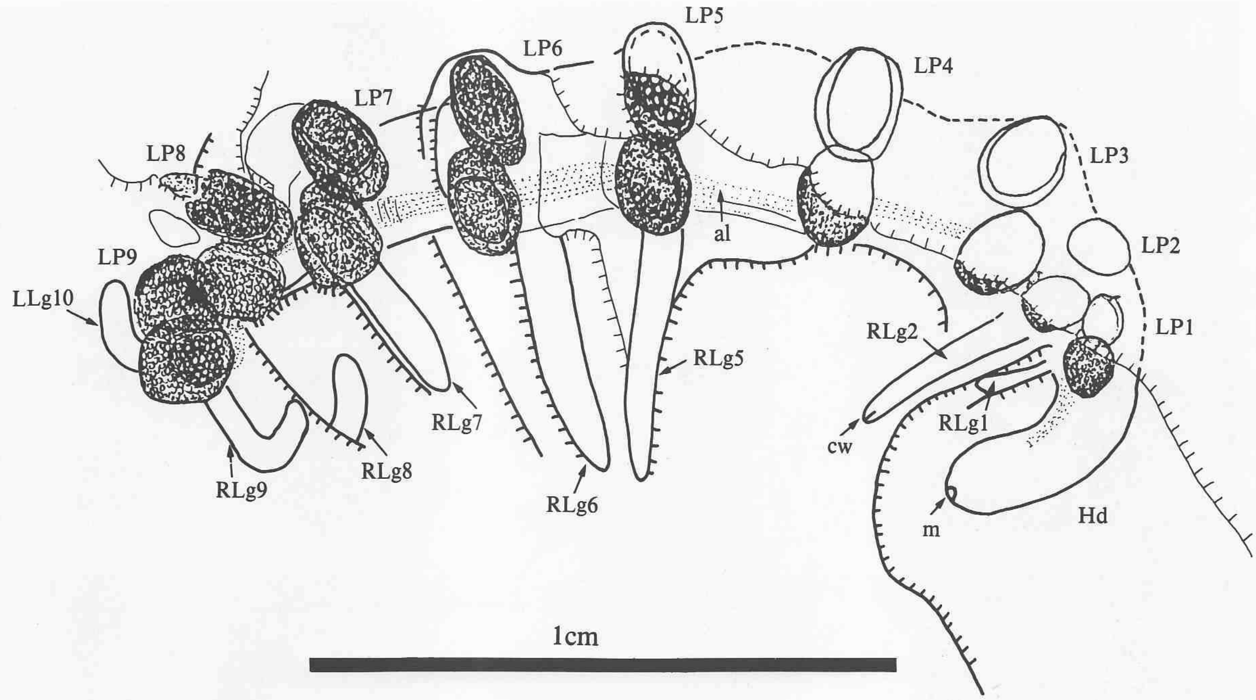


Plate 8

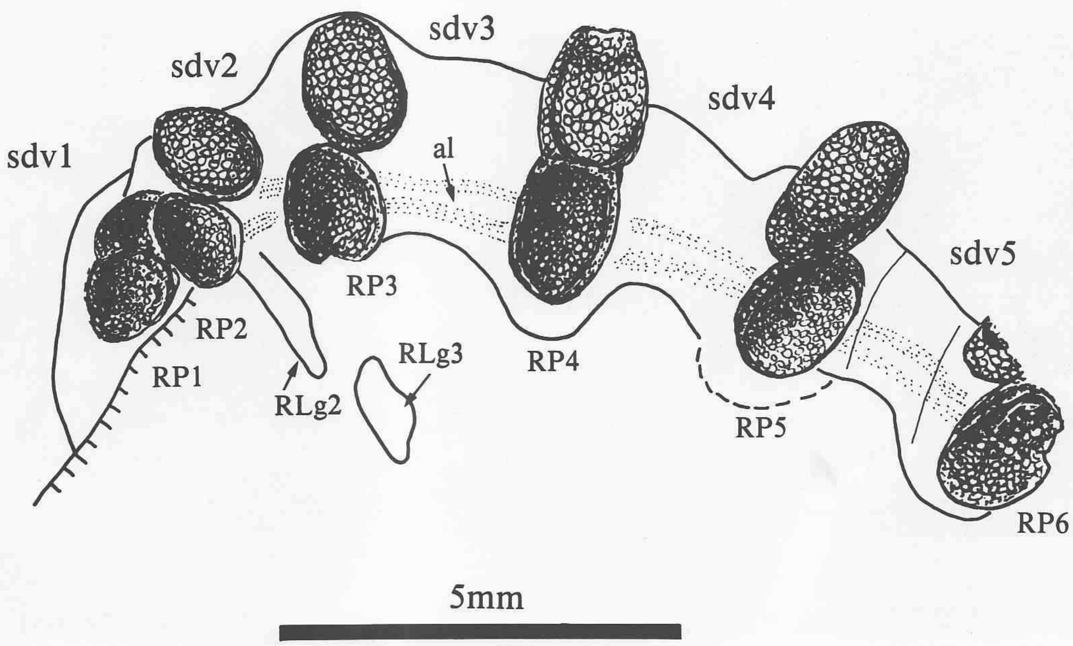
Figure 1. Part of ELRC 30049, MQA, X7.7, on upper surface of a slab, subdorsal specimen, NW, see text-figure 20.

Figure 2. Enlargement of the posterior trunk portion in the part of ELRC 30049, showing double plates, X13.7, NW.

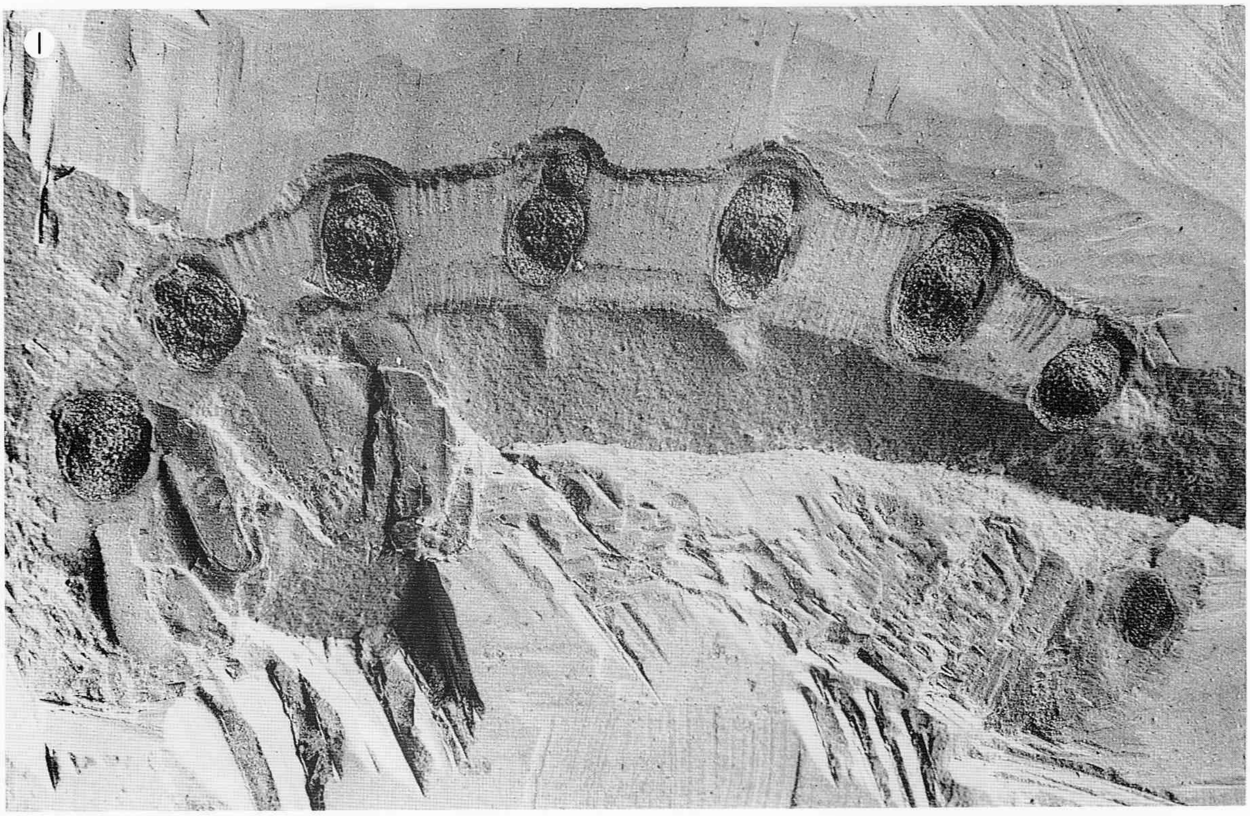
Figure 3. Counterpart of ELRC 30049, X12.3, on the underside of a slab, NE; see text-figure 21.



Text-figure 20



Text-figure 21



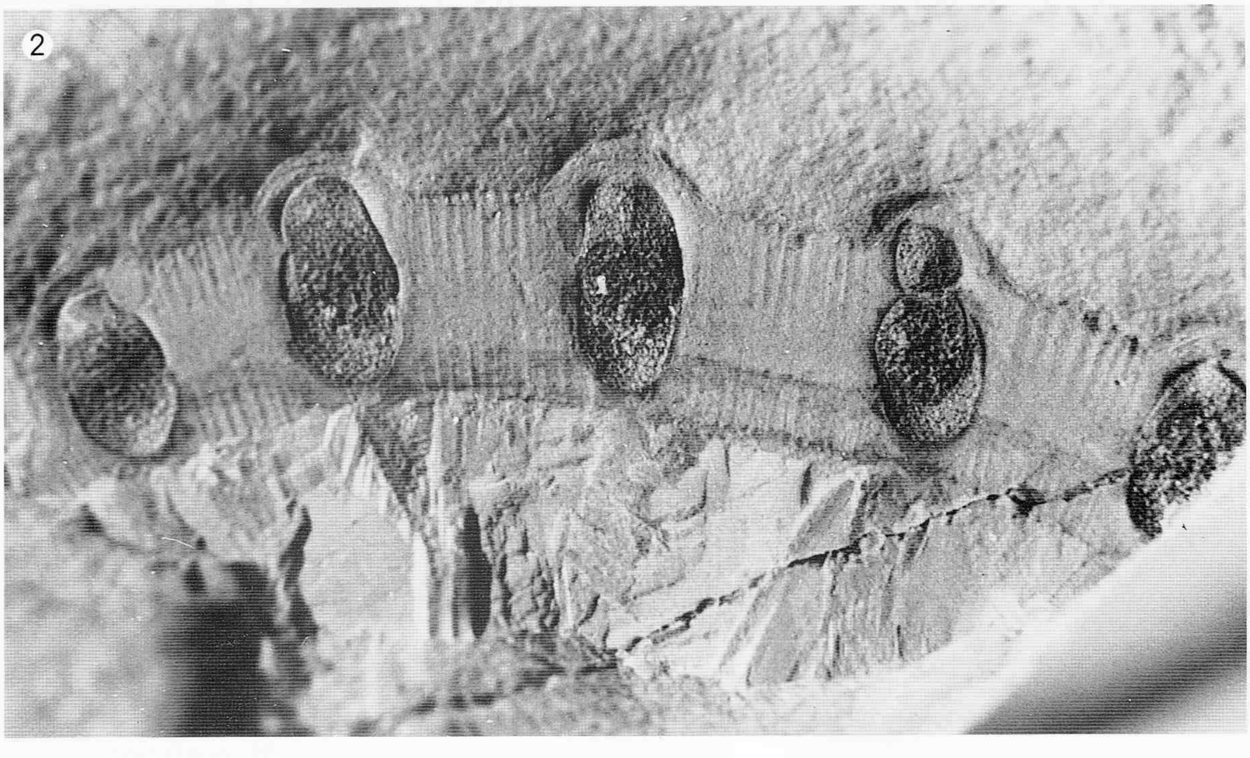
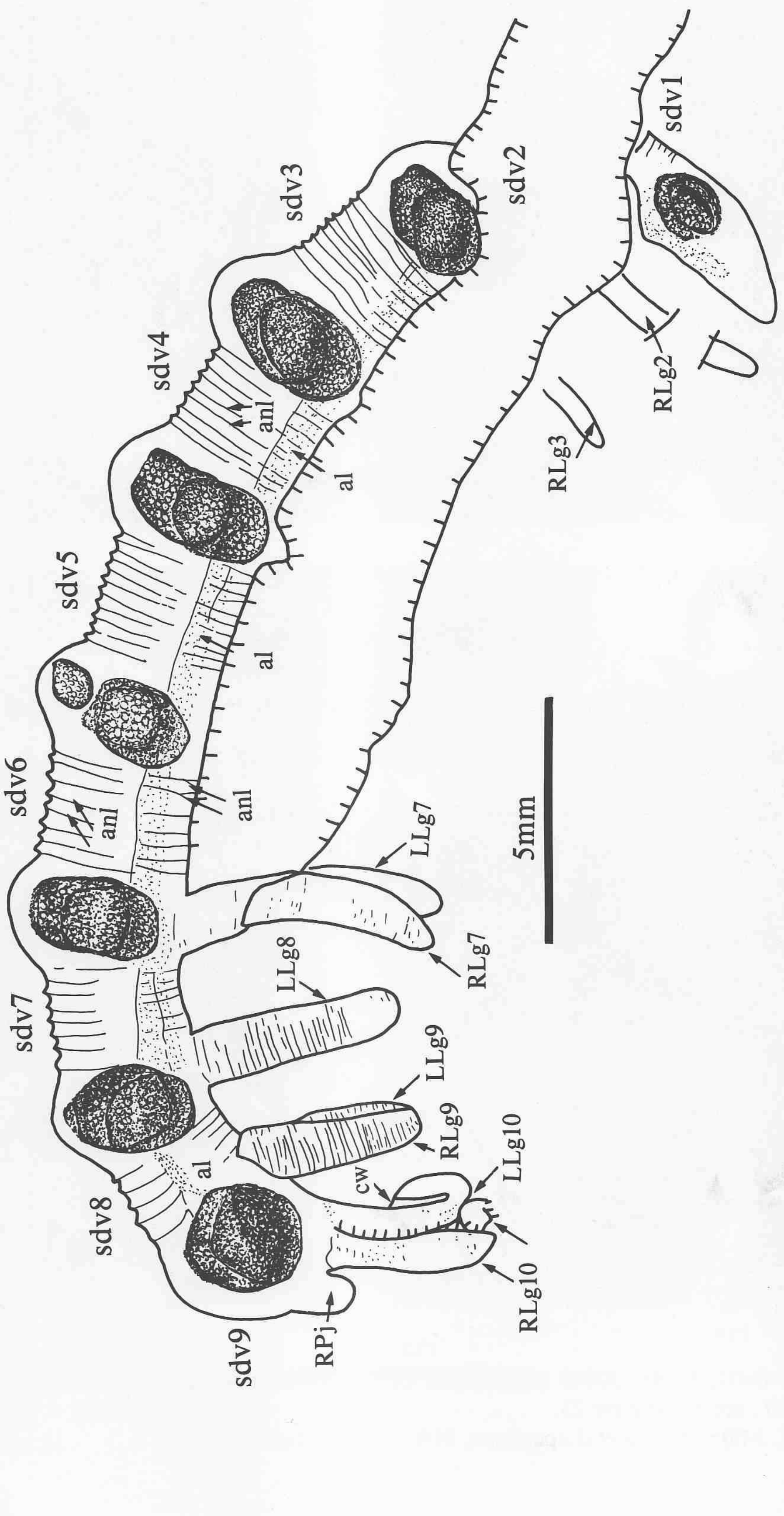


Plate 9
Figure 1. Part of ELRC 30027, MQ1, X5.4, a lateral specimen, NE; see text-figure 22.
Figure 2. Counterpart of ELRC 30027, MQ1, X8, NE.



Text-figure 22

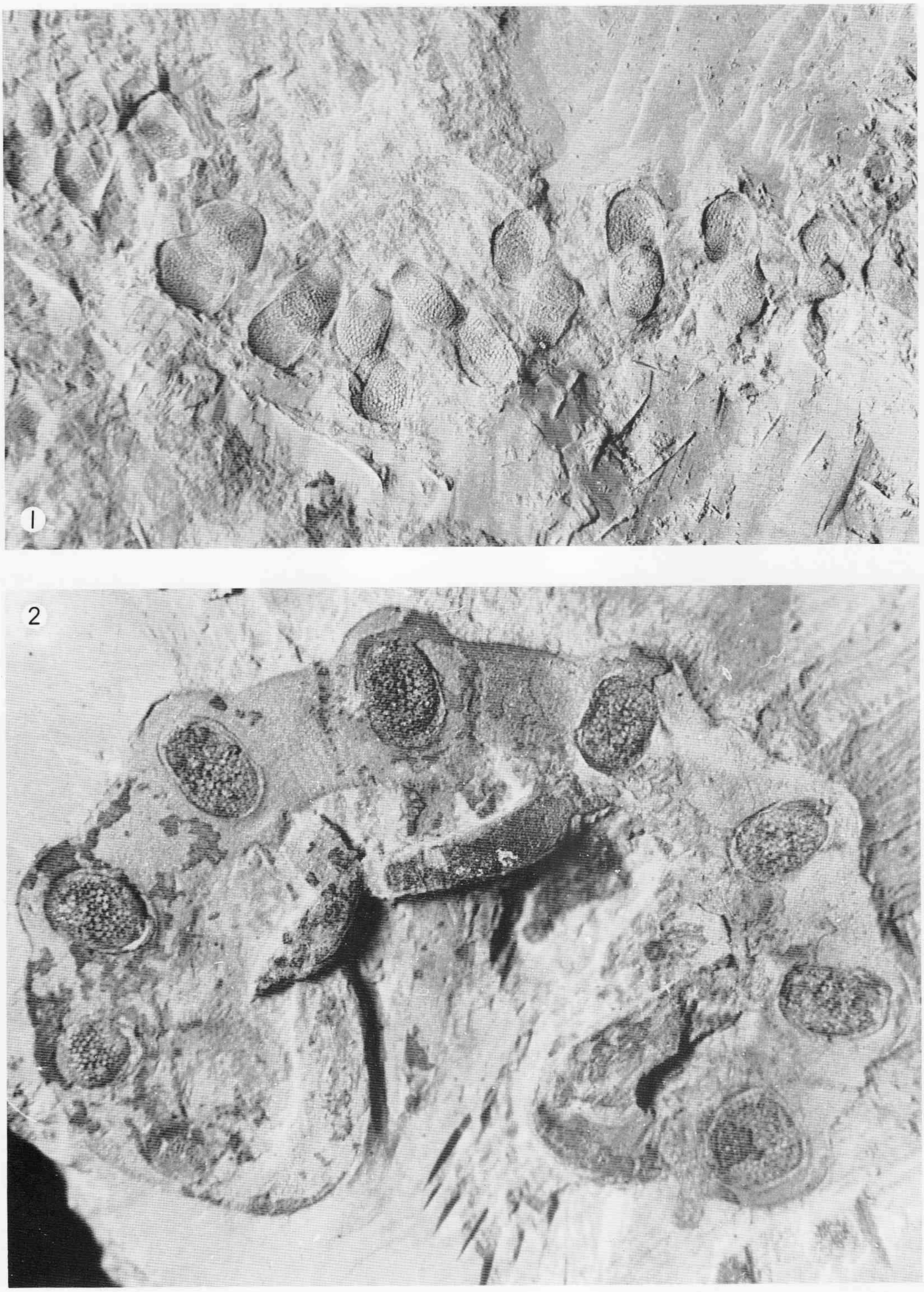
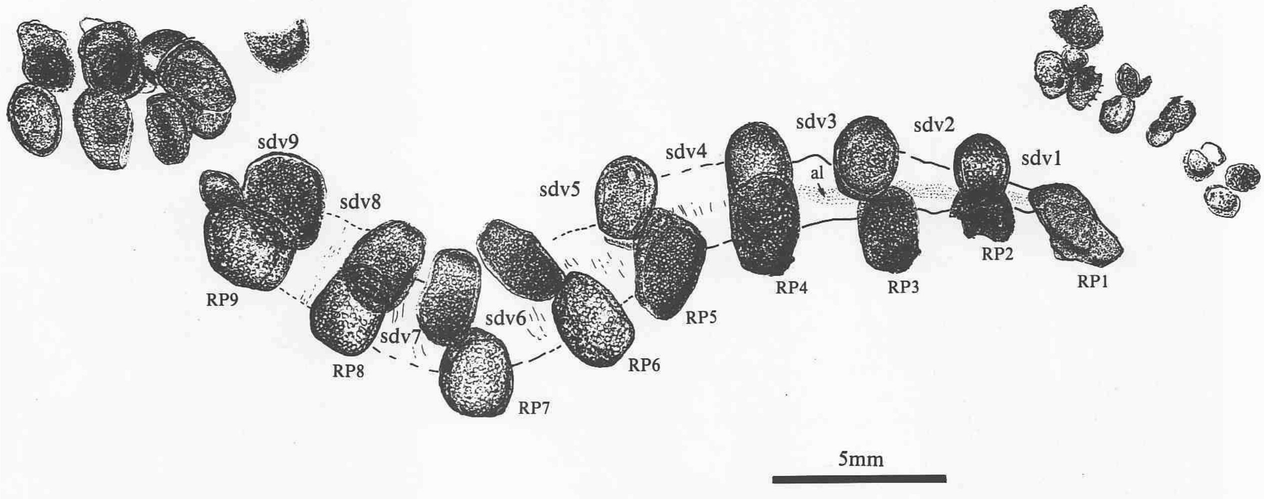


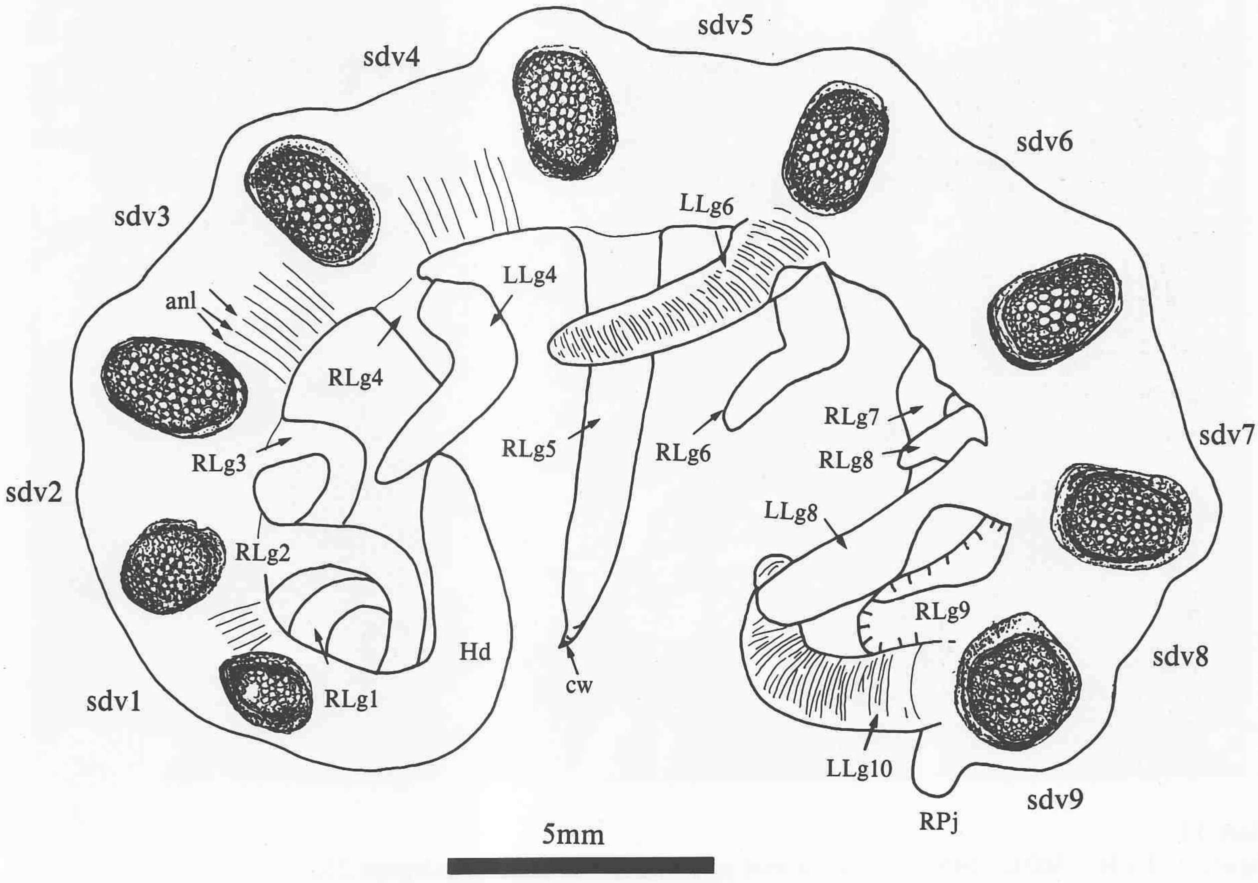
Plate 10

Figure 1. ELRC 30039 (left), ELRC 30040 (right), and ELRC 30041 (middle), MAQ, X4.3, subdorsal specimen, NW; see text-figure 23.

Figure 2. ELRC 30008, MQ1, X7, lateral specimen, NW; see text-figure 24.



Text-figure 23



Text-figure 24

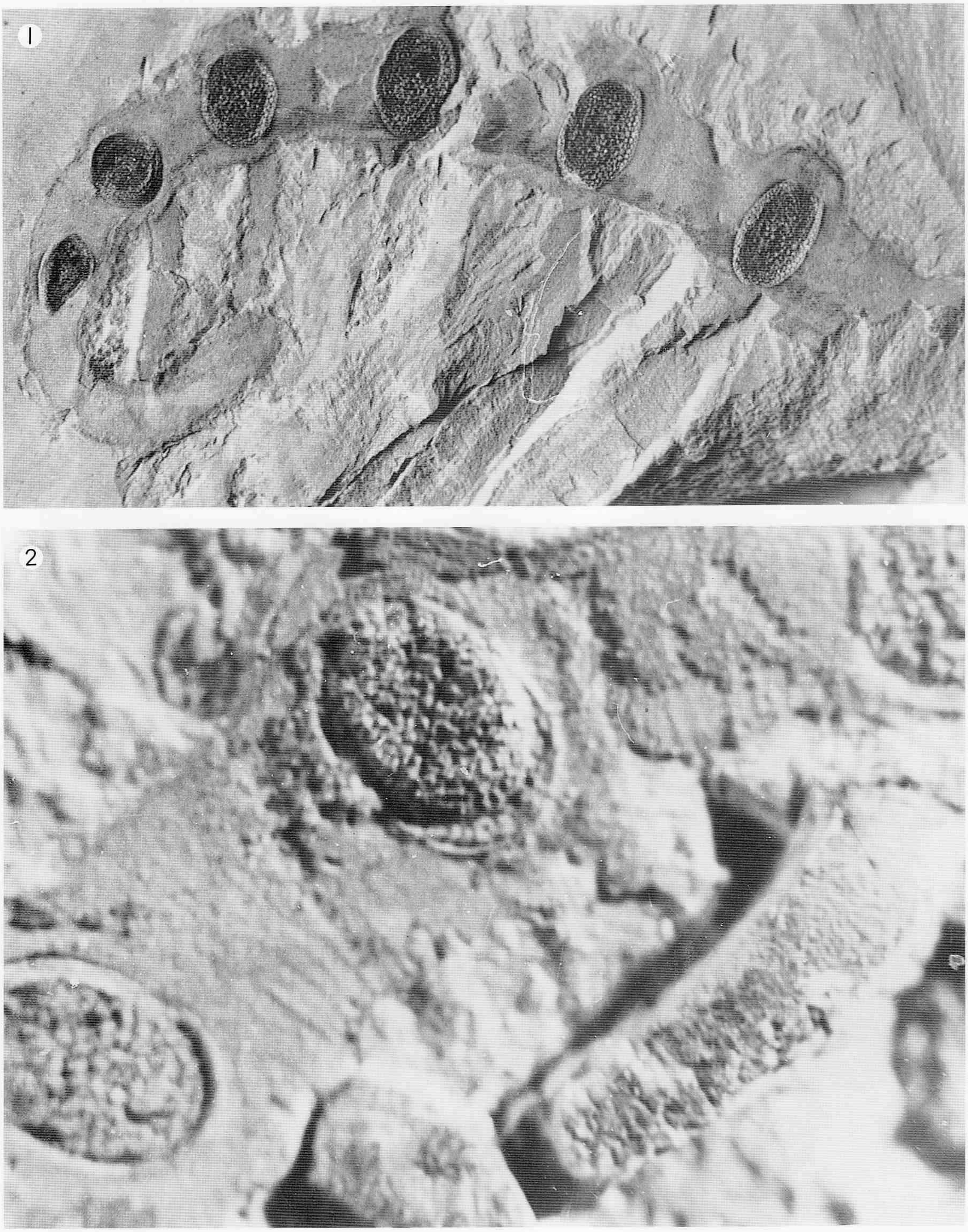
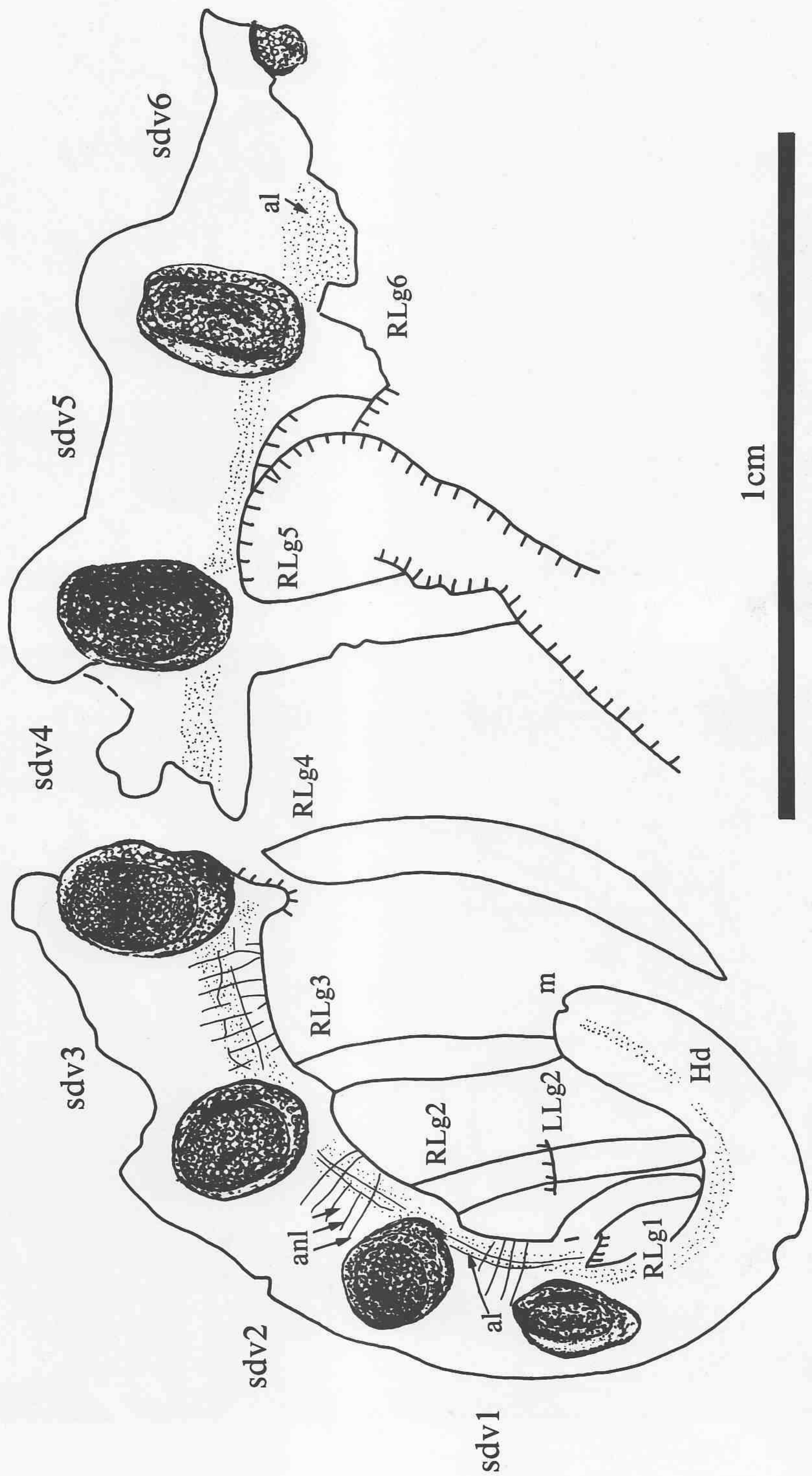


Plate 11

Figure 1. ELRC 30017, MN5, X7.4, lateral specimen, NW; see text-figure 25.

Figure 2. Enlargement of ELRC 30008 showing annulations on the external surface of the trunk and leg, X17, ENE.



Text-figure 25

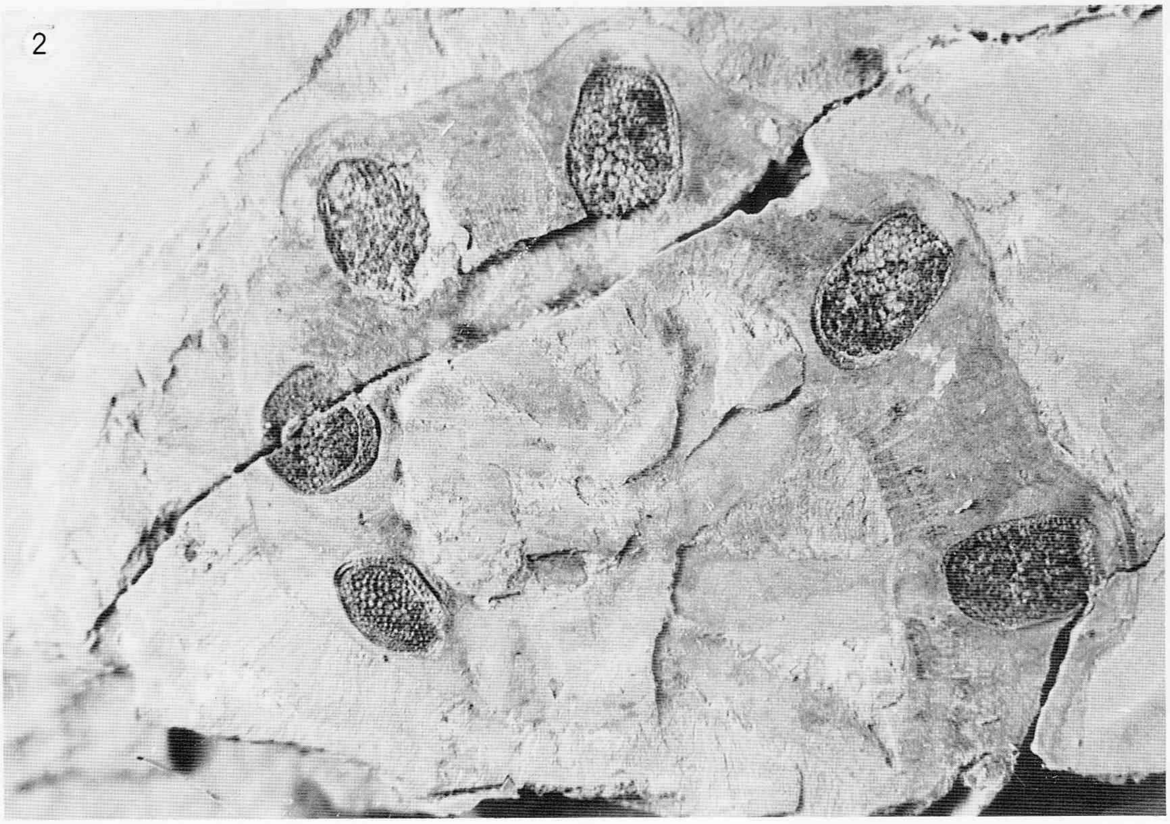
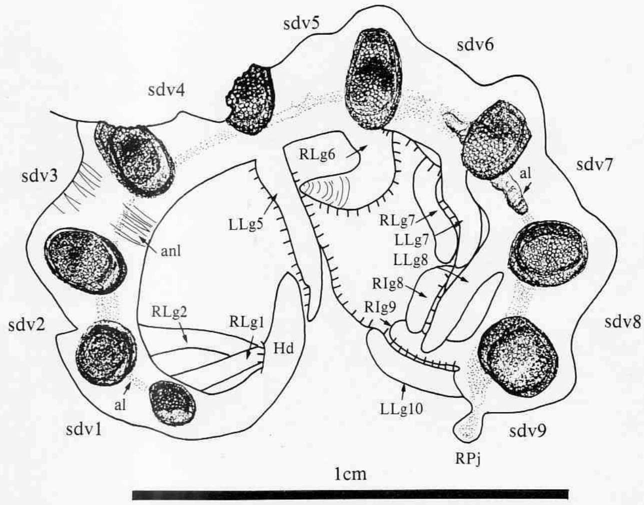
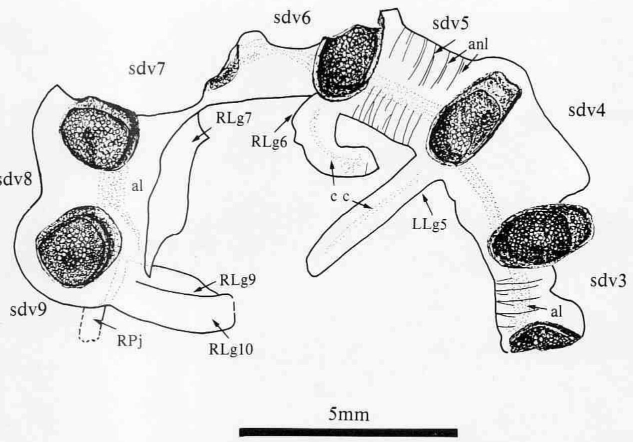


Plate 12

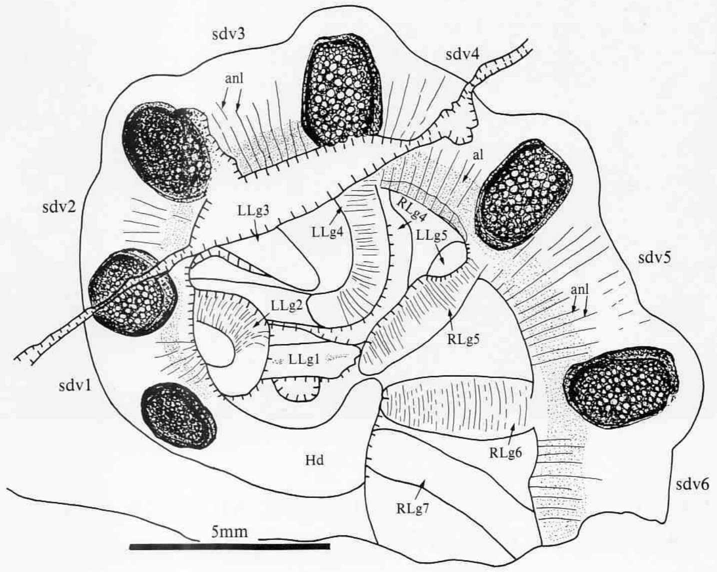
Figure 1. Part of ELRC 30001, MN5, X10, lateral compaction, WNW; see text-figs. 26 and 27.
Figure 2. ELRC 30016, MQ1, X7, lateral specimen, NW; see text-figure 28.



Text-figure 26

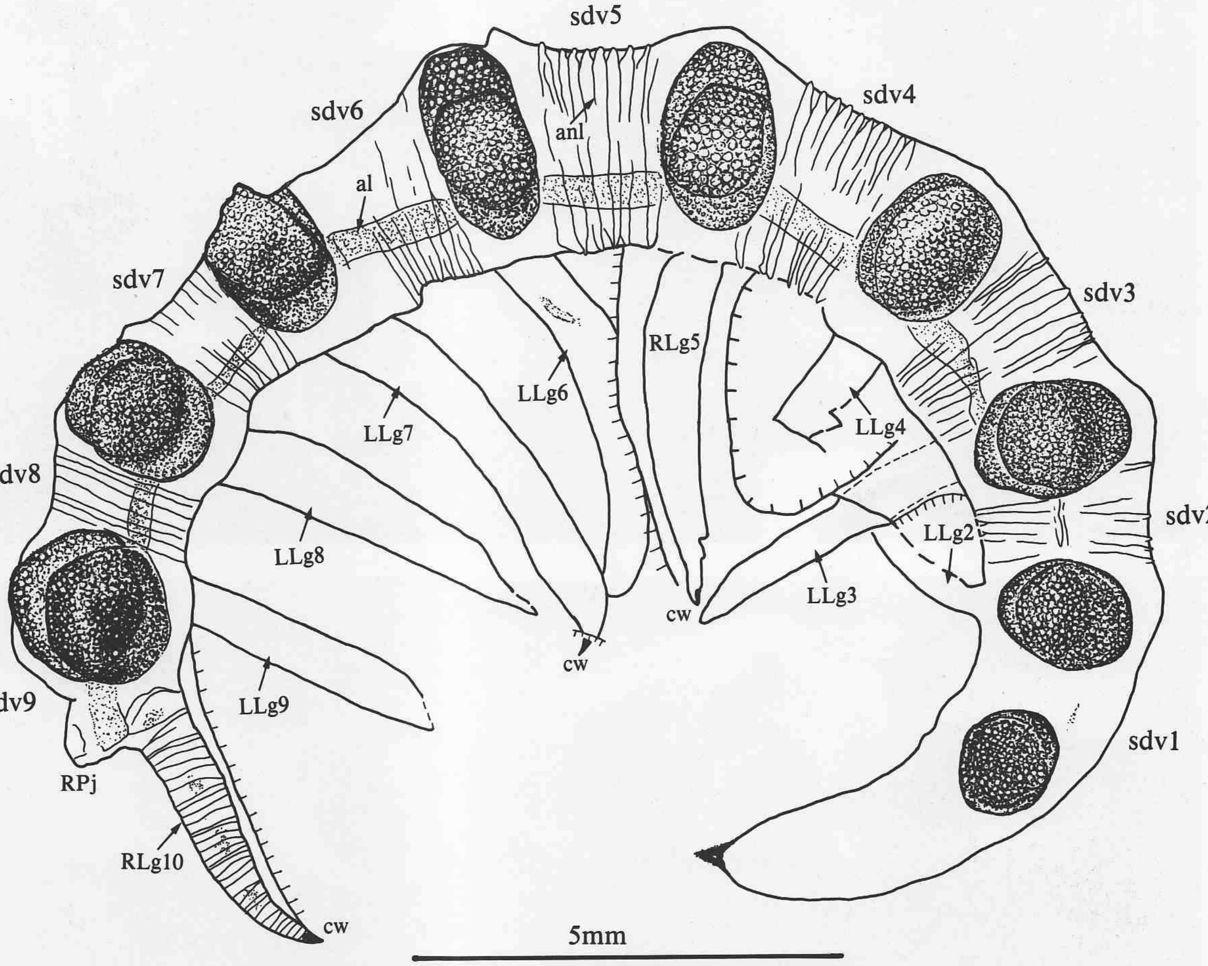


Text-figure 27



Text-figure 28

Plate 13
Figure 1. ELRC 30033 (left) and ELRC 30034 (right), MQ1, X9, NW.
Figure 2. ELRC 30009, MQ1, X10.5, NW; see text-figure 29.



Text-figure 29

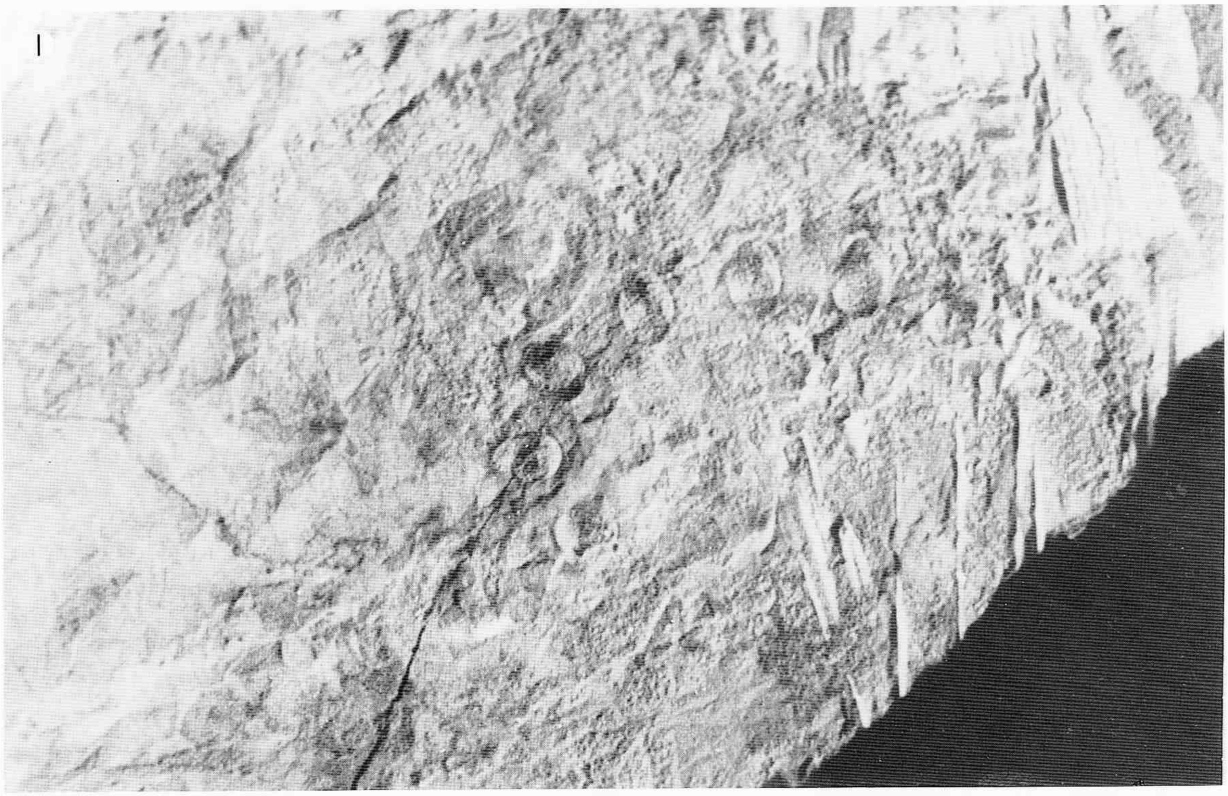
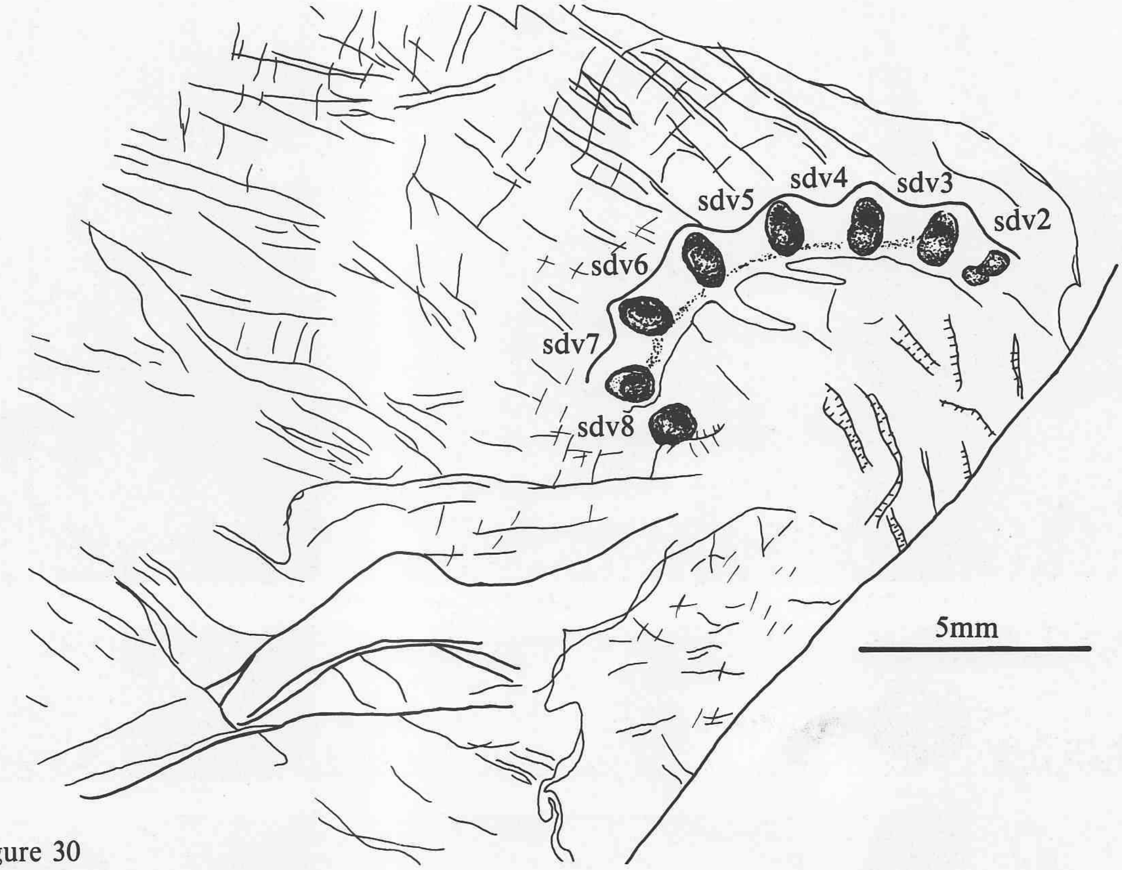
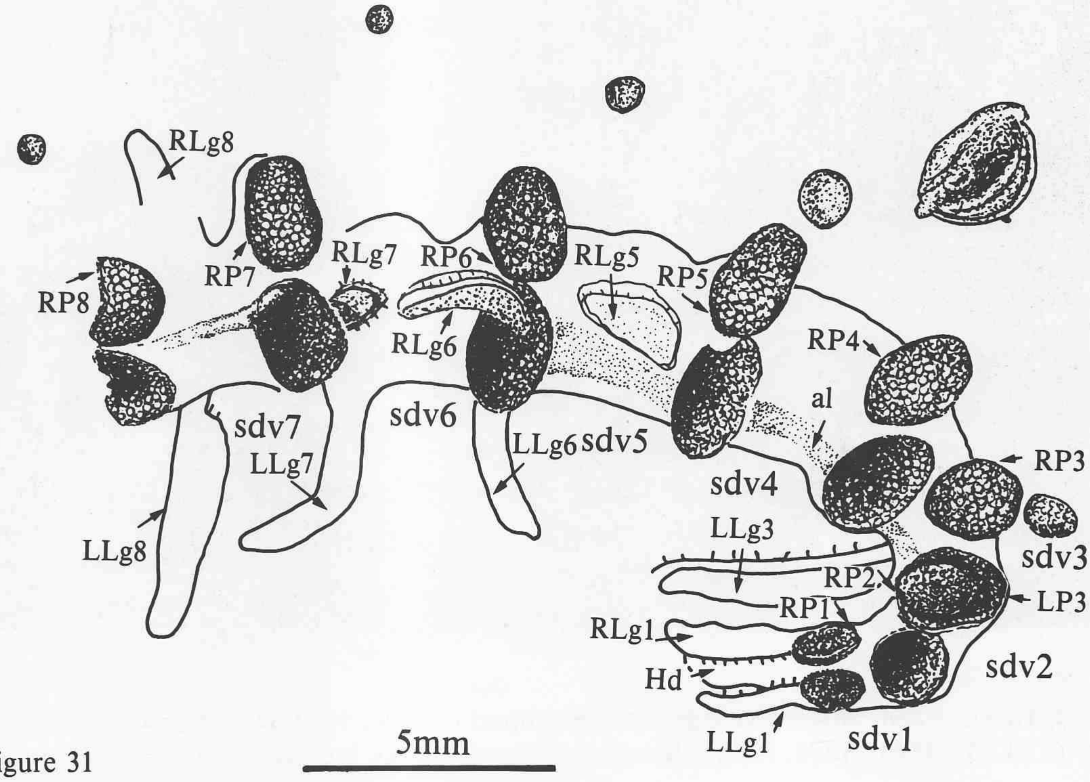


Plate 14

Figure 1. A *Microdictyon*, ELRC 30046, directly attaching to an *Eldonia*, MQA, X9, NW; see text-figure 30.
Figure 2. ELRC 30022, MQA, X12, subdorsal specimen, NW; see text-figure 31.

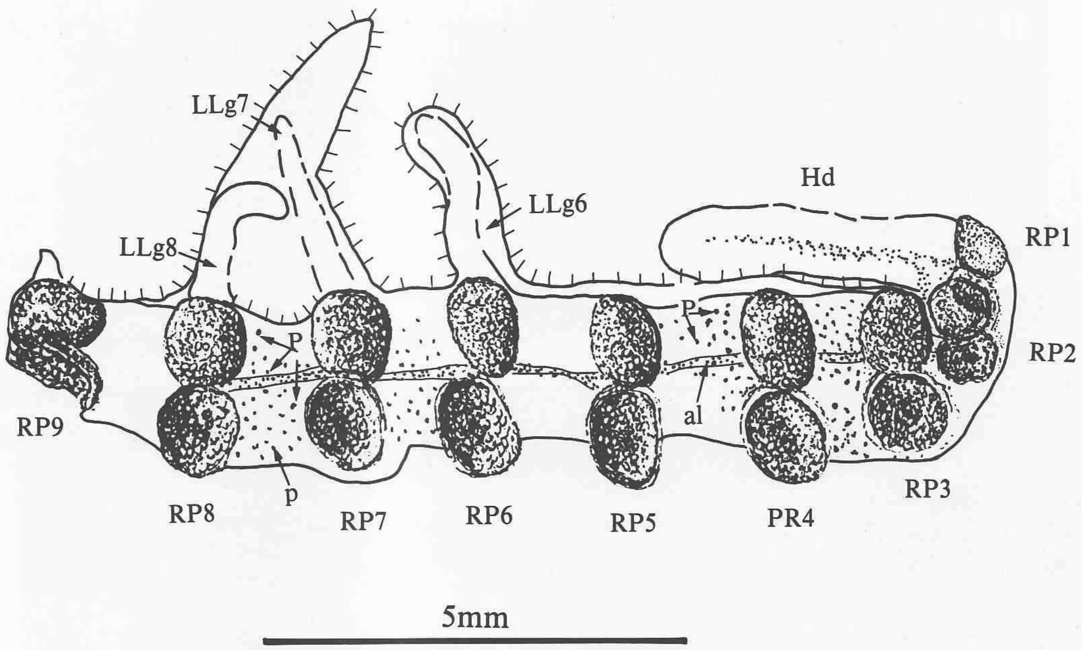


Text-figure 30

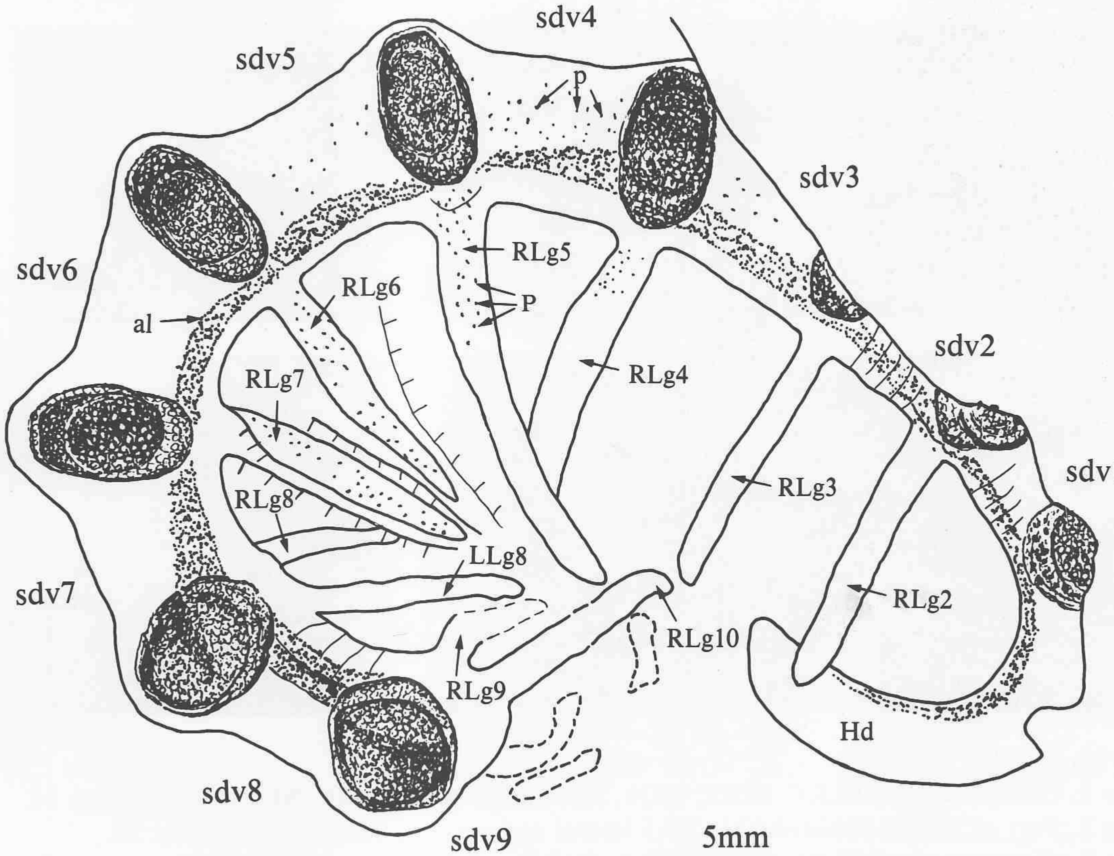


Text-figure 31

Plate 15
Figure 1. ELRC 30031, MQA, X15, subdorsal compaction, NE; see text-figure 32.
Figure 2. ELRC 30061, MQ1, X10.7, lateral specimen, NE; see text-figure 33.



Text-figure 32



Text-figure 33

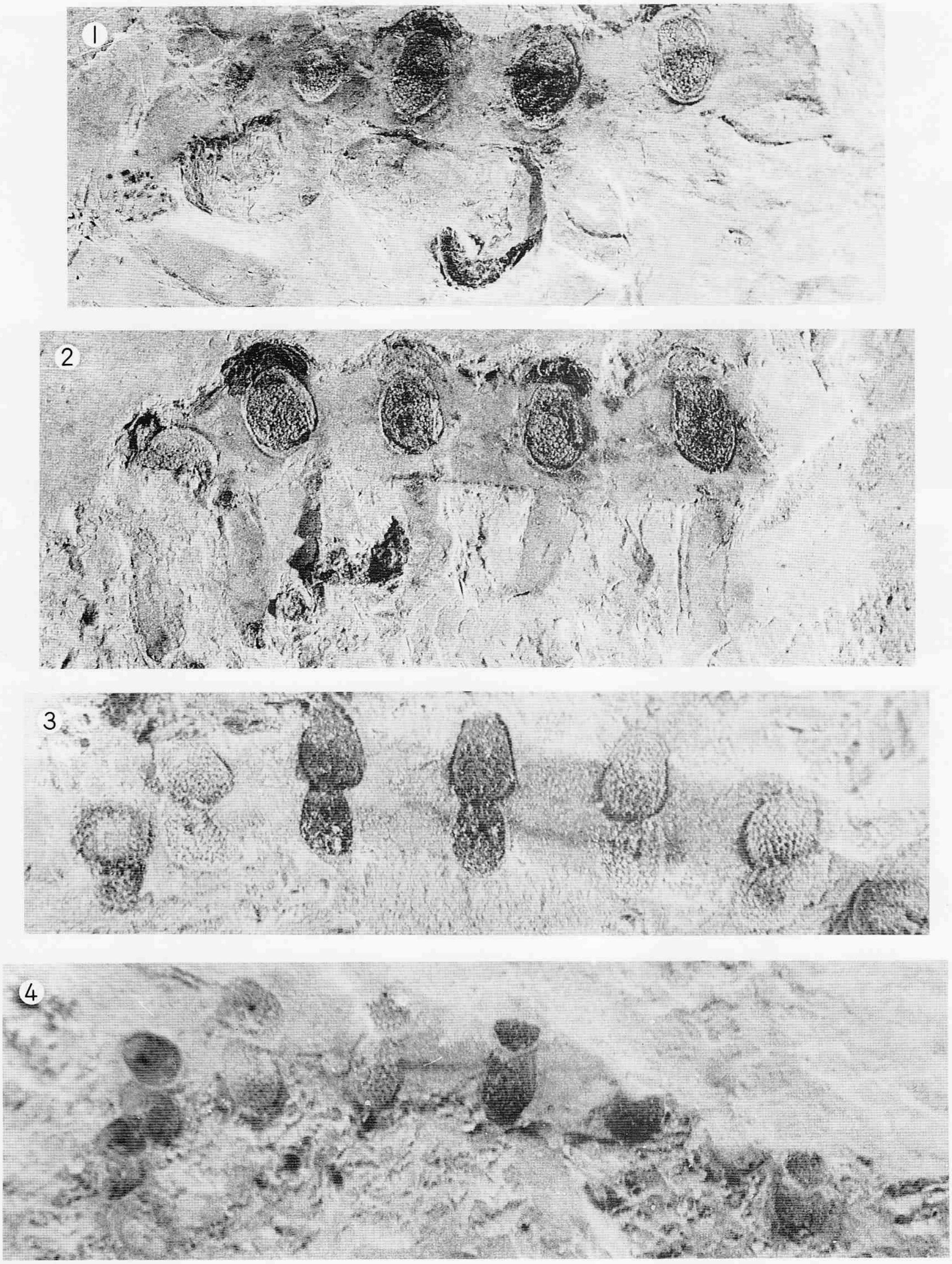
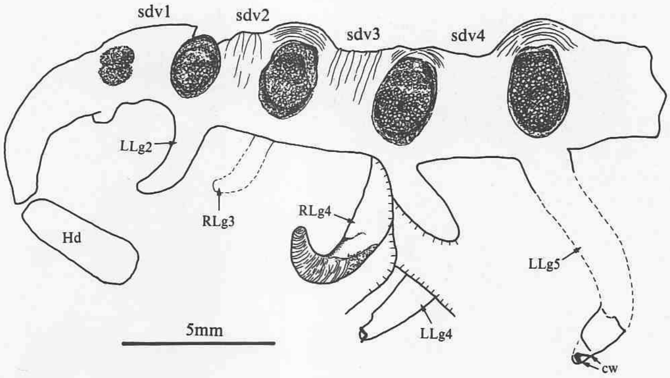
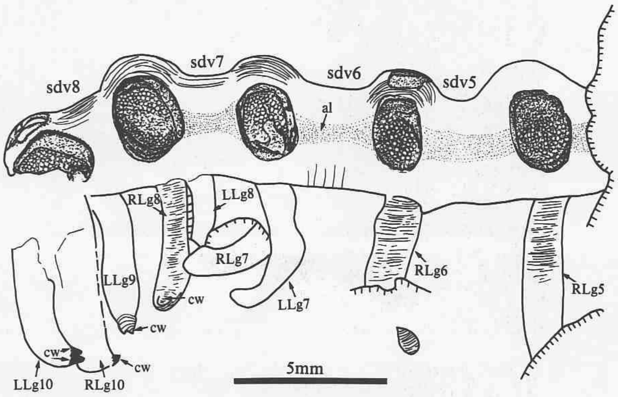


Plate 16

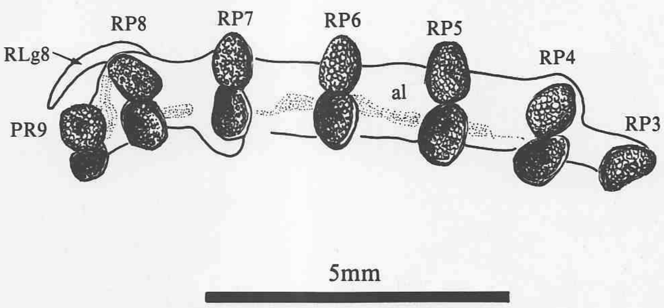
Figure 1. Counterpart of ELRC 30021, MQ1, X5, lateral compaction, NE; see text-figure 34.
Figure 2. Part of ELRC 30021, MQ1, X5.5 lateral compaction, NE; see text-figure 35.
Figure 3. Counterpart of ELRC 30036, MQA, X13.5, subdorsal compaction, NE; see text-figure 36.
Figure 4. Part of ELRC 30036, X11, MQA, subdorsal compaction, NW; see text-figure 37.



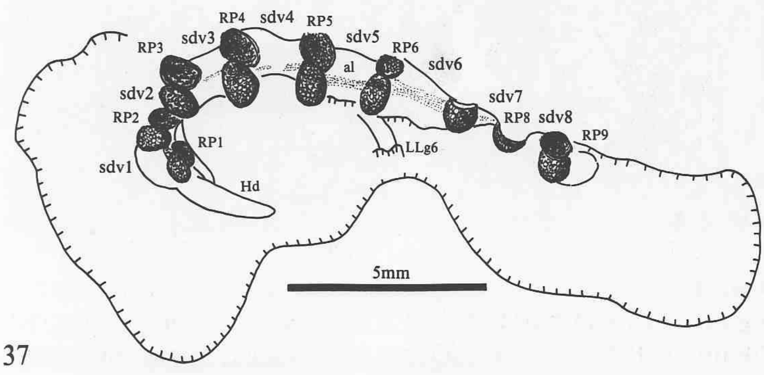
Text-figure 34



Text-figure 35



Text-figure 36



Text-figure 37

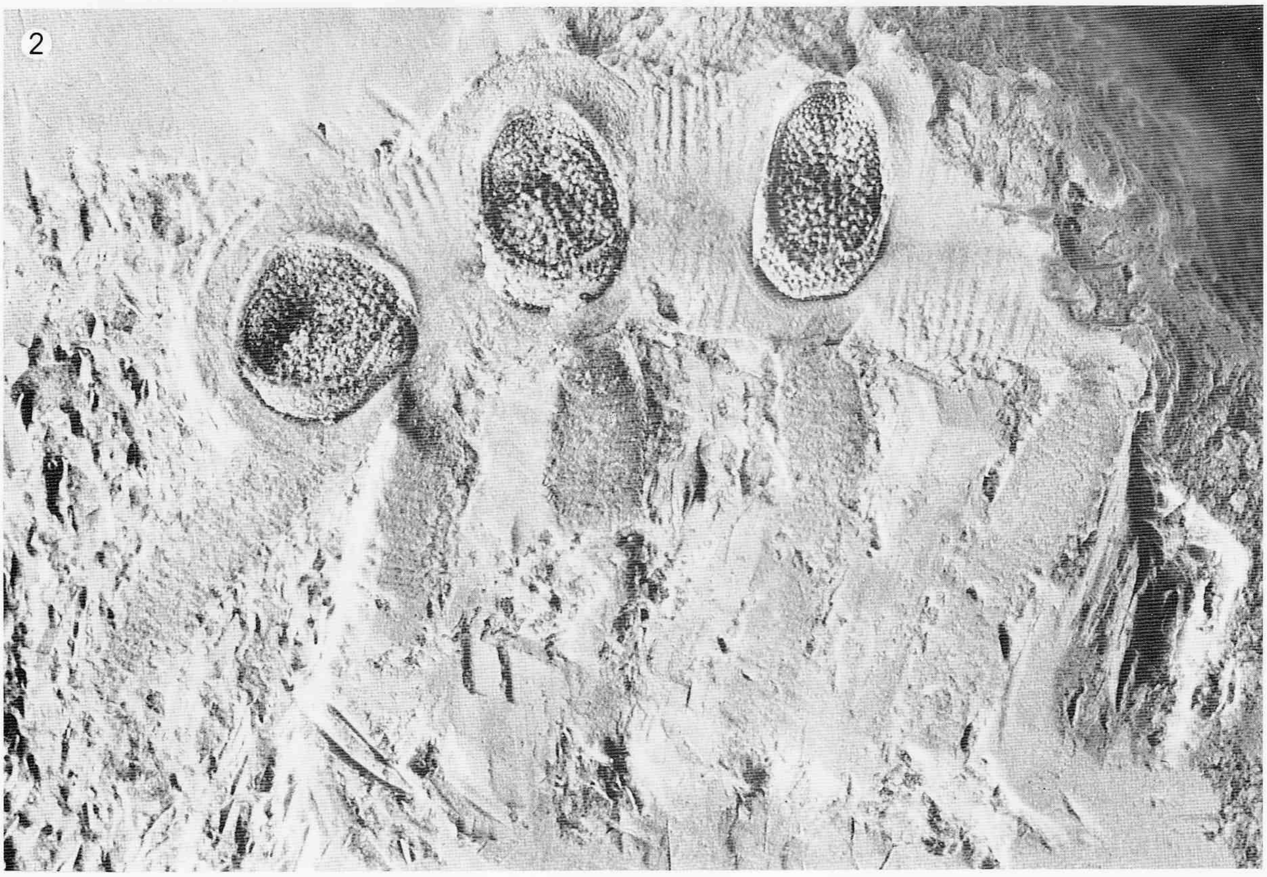
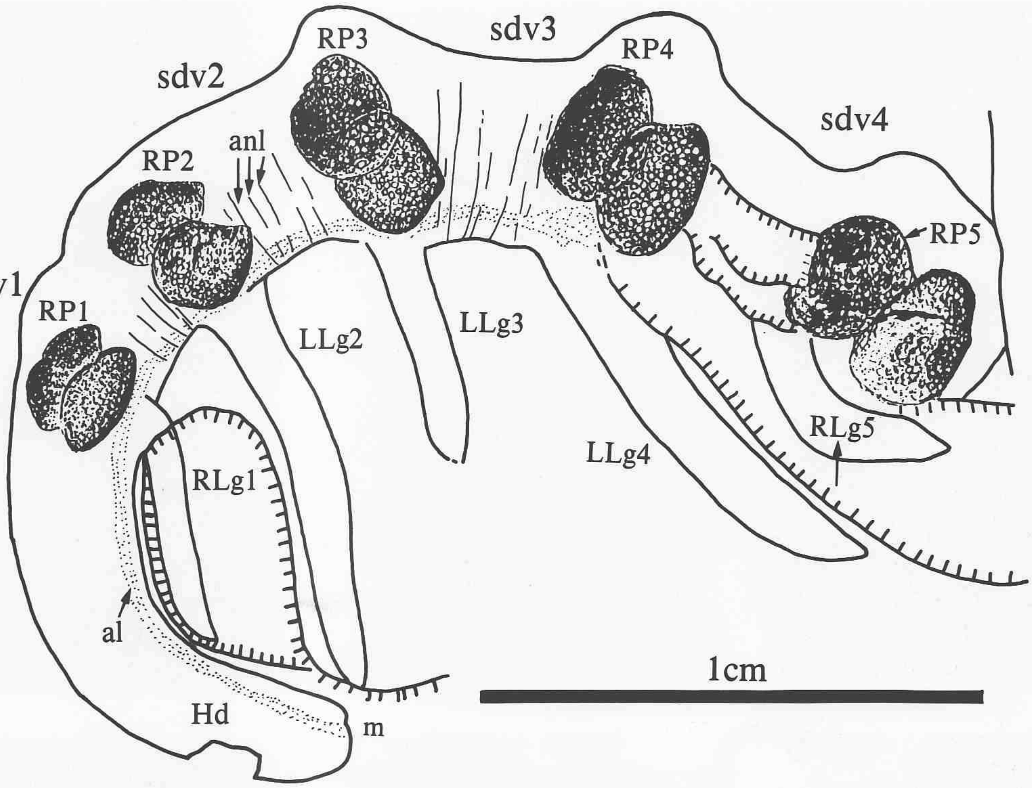
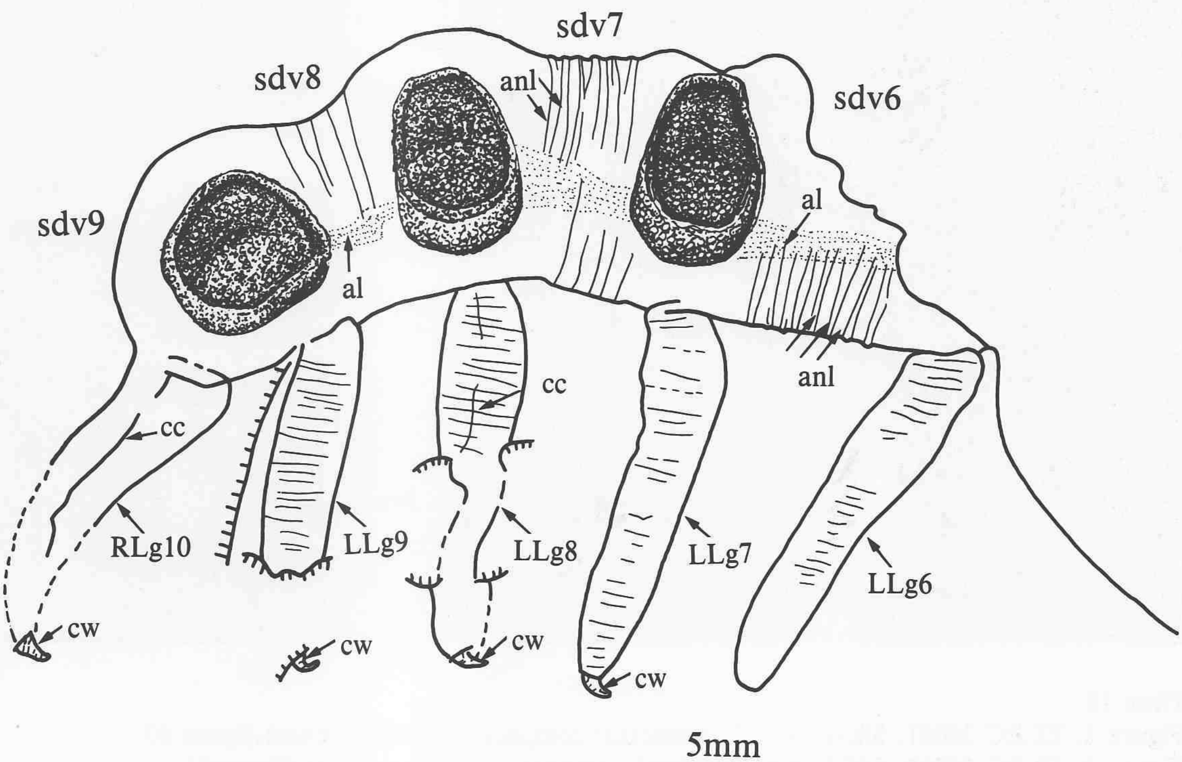


Plate 17
Figure 1. ELRC 30011, MN6, X8.2 subdorsal compaction, NW; see text-figure 38.
Figure 2. ELRC 30010, MQ1, X10, lateral compaction, NW; see text-figure 39.

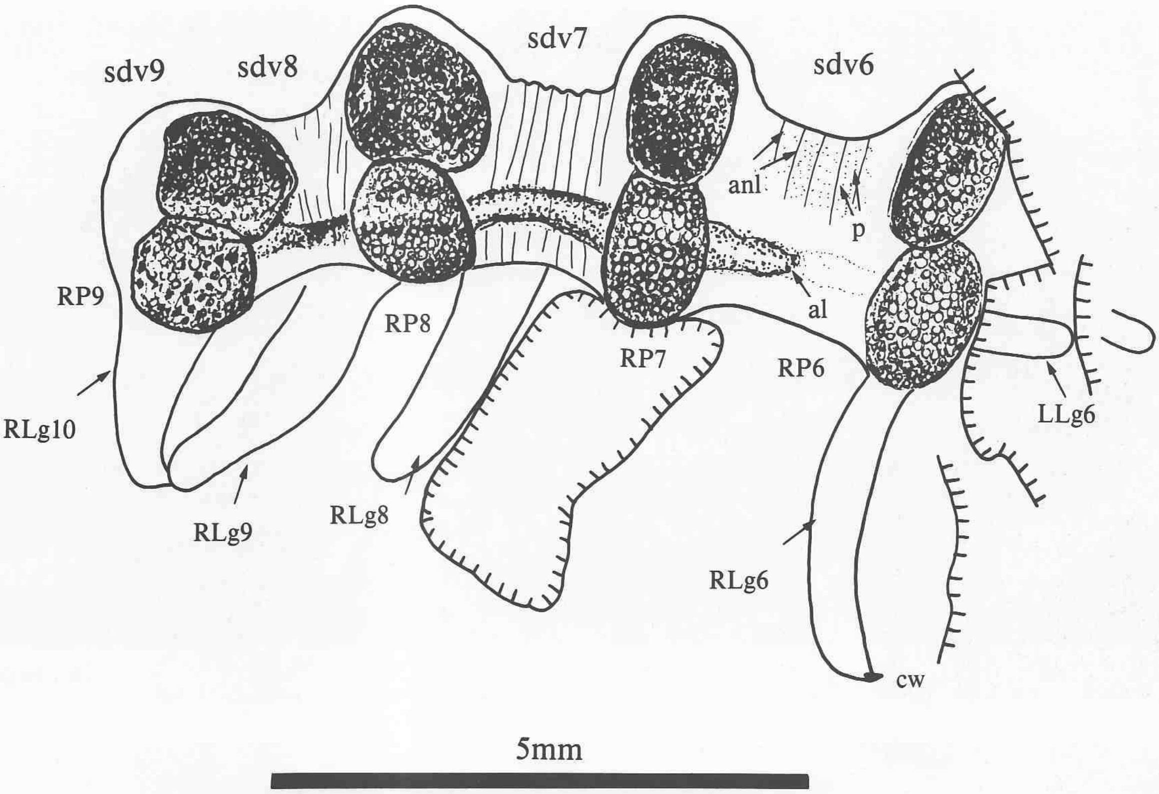


Text-figure 38

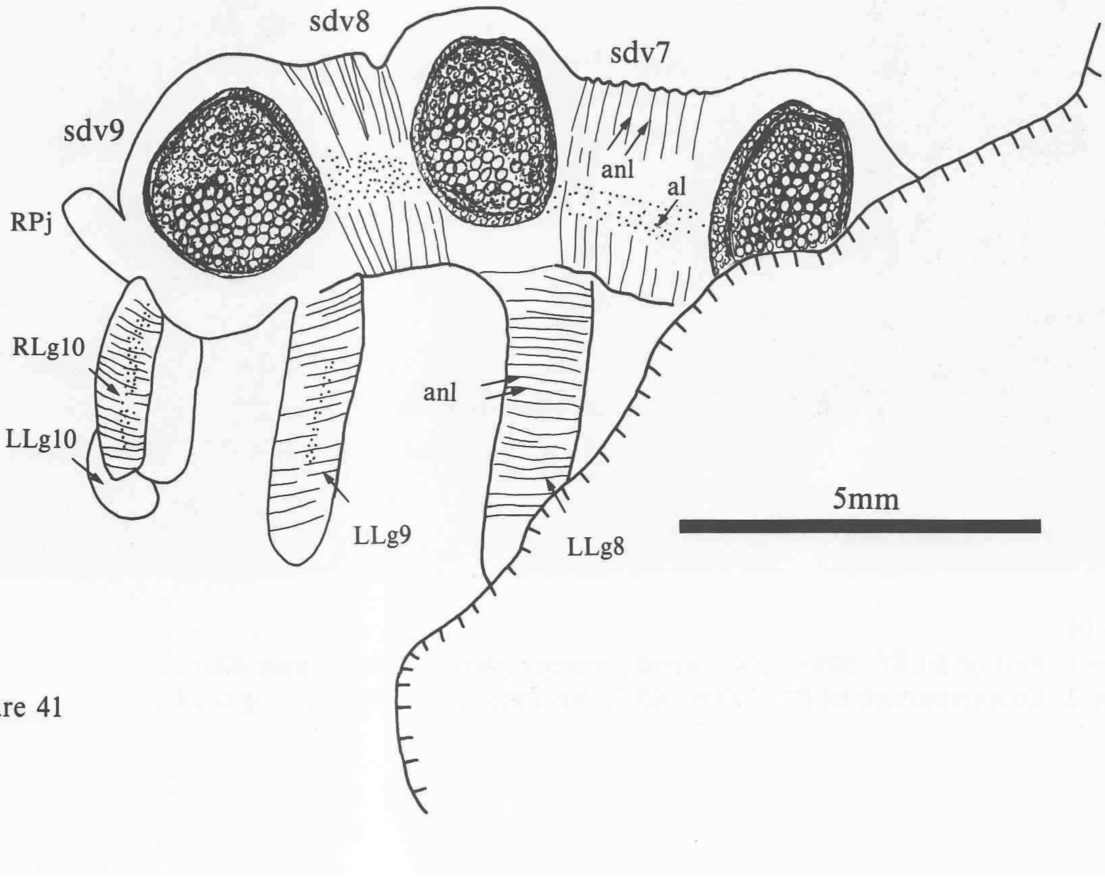


Text-figure 39

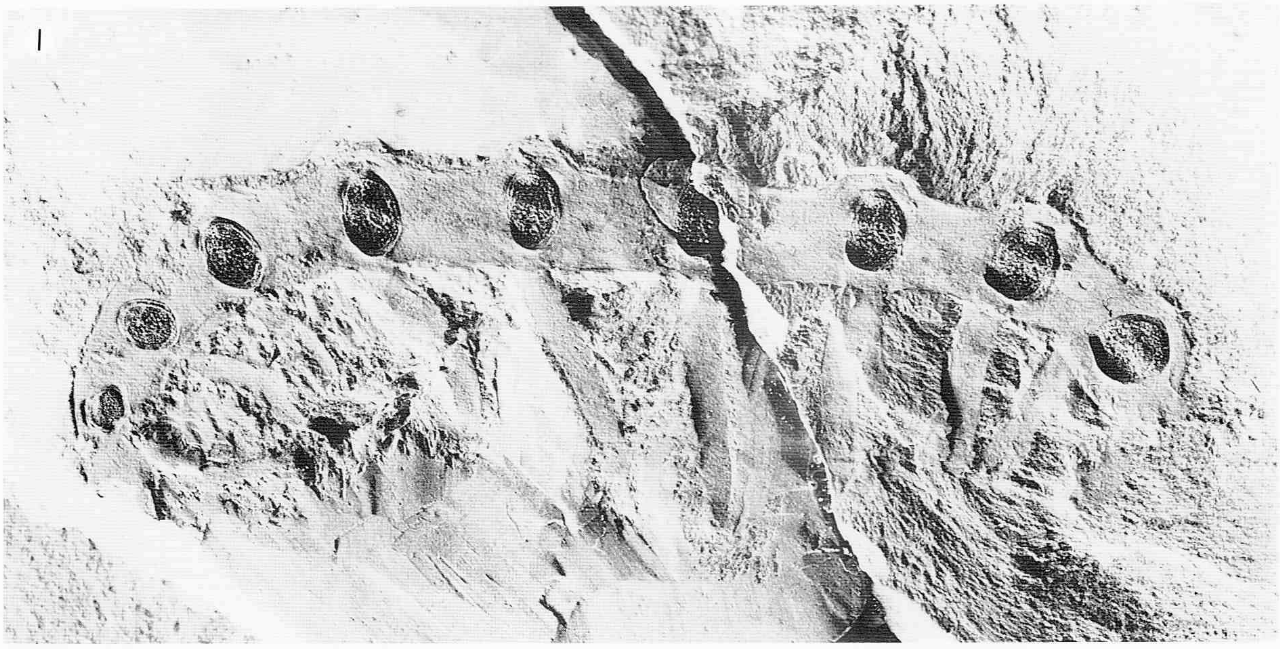
Plate 18
Figure 1. ELRC 30051, MQ1, X10.7, subdorsal compaction, NW, see text-figure 40.
Figure 2. ELRC 30015, MQ1, X11.7, lateral compaction, NW; see text-figure 41.



Text-figure 40



Text-figure 41



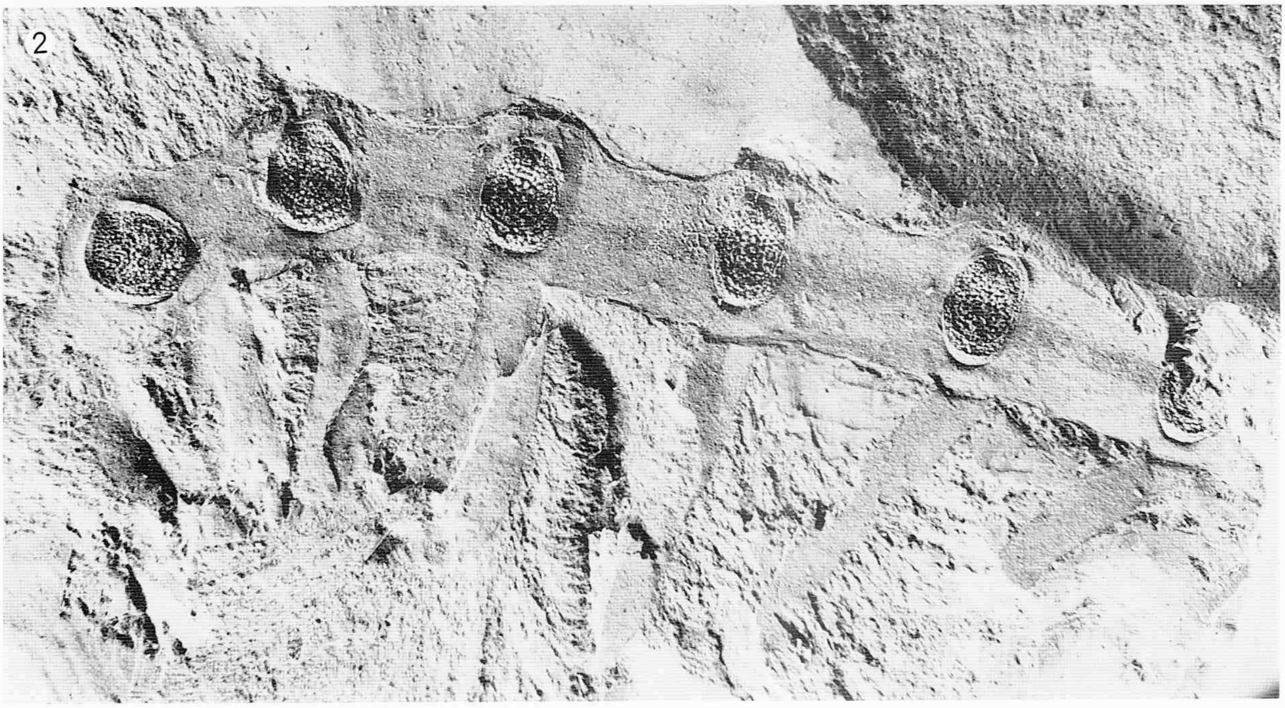
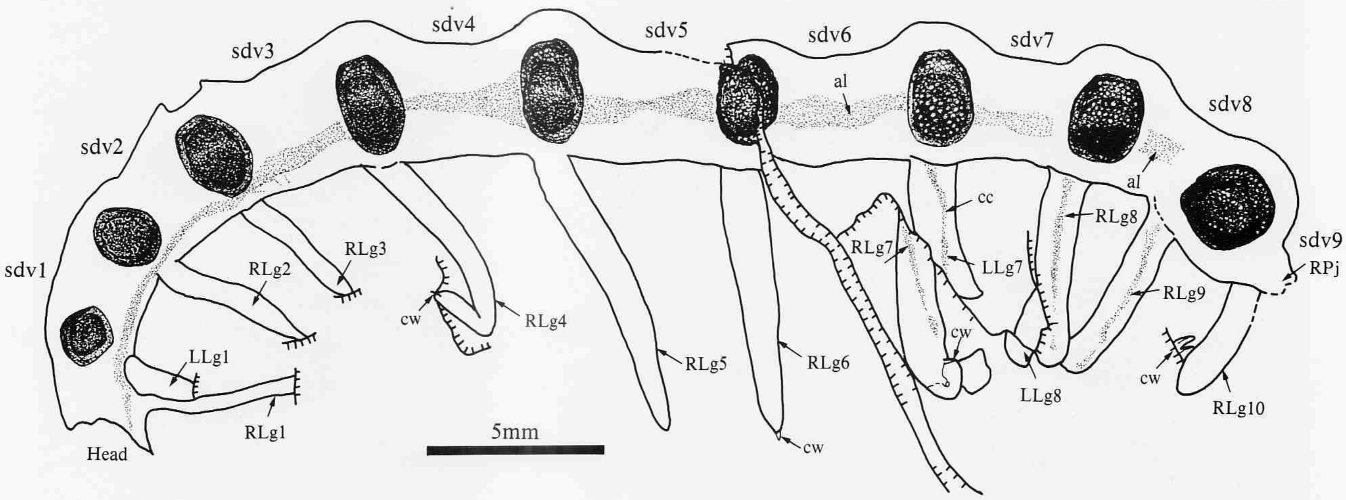


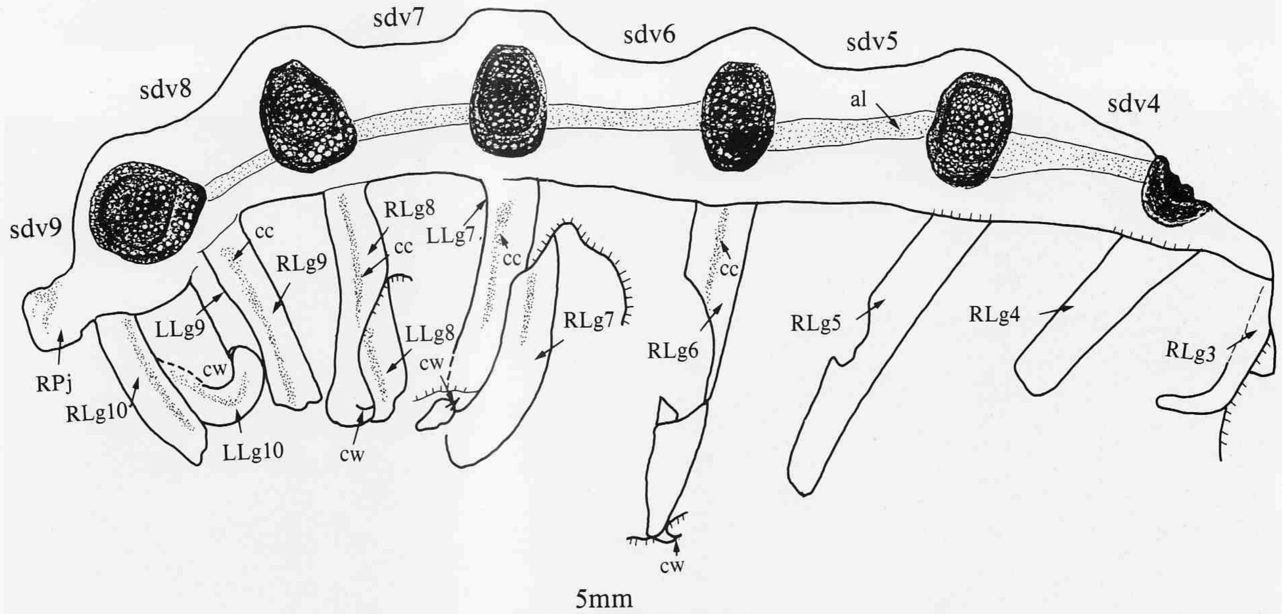
Plate 19

Figure 1. Part of ELRC 30006, X4, lateral specimen, NW; see text-figure 42.

Figure 2. Counterpart of ELRC 30006, X5.7, NW; see text-figure 43.



Text-figure 42

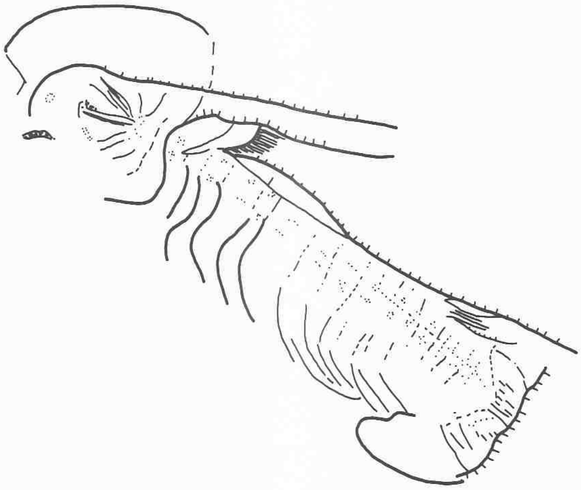


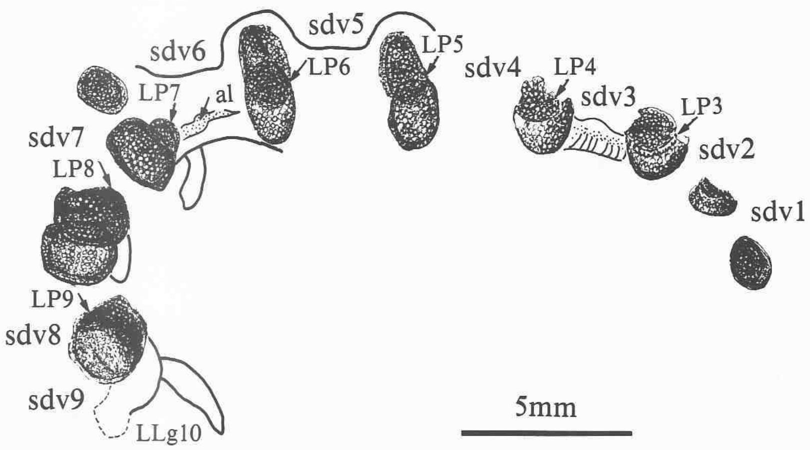
Text-figure 43

Plate 20

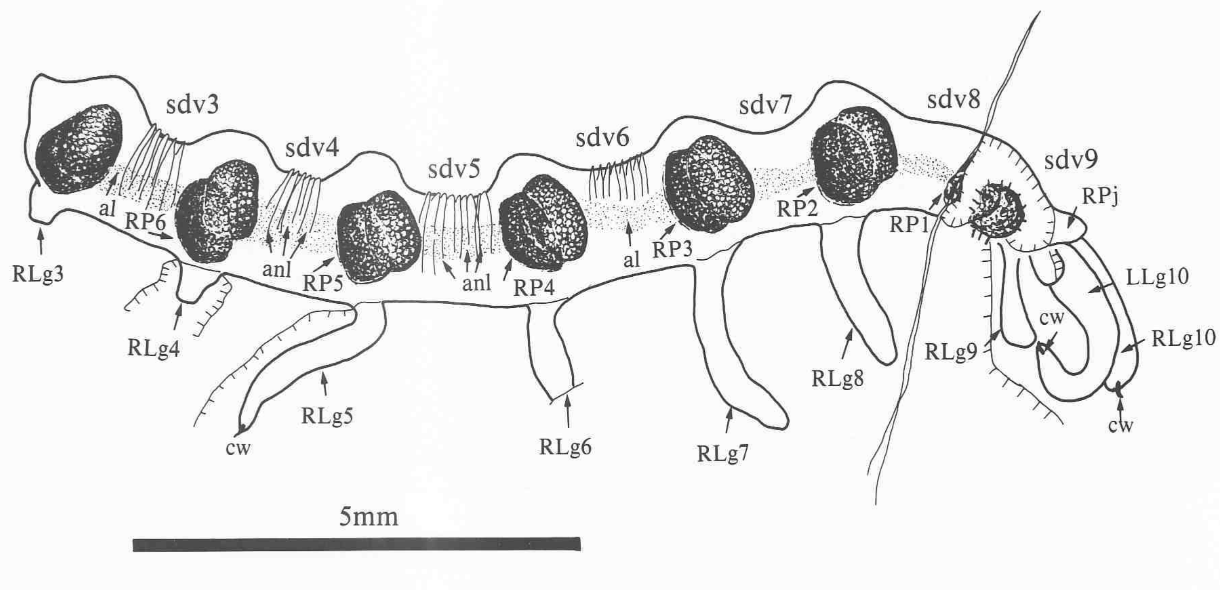
Figure 1. Part of ELRC 30042, X7, subdorsal compaction, NW; see text-figure 44.

Figure 2. ELRC 30005, X6.8, a sublateral specimen, showing a gentle dorsal curvature, NW; see text-figure 45.





Text-figure 44



Text-figure 45