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BURROWS OF ENTEROPNEUSTA IN MUSCHELKALK (MIDDLE TRIASSIC) OF THE HOLY CROSS MOUNTAINS, POLAND

Abstract. — Traces of burrowing organisms from Lower Muschelkalk carbonate sediments of the Holy Cross Mountains (Góry Świętokrzyskie) interpreted as burrow systems of enteropneusts, have been described. Morphological and palaeoecological analysis of Triassic forms based on the comparison with the burrows of Recent enteropneusts is given. The presence of many horizons with burrows of enteropneusts in the profiles of the Lower Muschelkalk deposits (Łukowa beds) and the lithological characters of these deposits seem to indicate that the sedimentation took place in a zone of the basin affected by the activity of tidal currents.

INTRODUCTION

During field studies on biofacies of the Mesozoic border of the Holy Cross Mountains (Góry Świętokrzyskie) many traces of burrowing organisms were found by the present writers in the Lower Muschelkalk sediments. After a close examination, it turned out that these structures might be almost unequivocally identified with burrow systems of Recent enteropneusts. The field observations covered the environs of Wincentów and Polichno in the western part of the Holy Cross region and outcrops of the Lower Muschelkalk in the southwestern limb of Zbrza anticline (Text-fig. 1).

According to a lithostratigraphical division of the Lower Muschelkalk in the Holy Cross Mountains (Senkowiczowa, 1957, 1959, 1961), the burrows observed occur primarily in Łukowa beds (Text-fig. 1). The most important aim of this work was to describe and interpret the burrows of enteropneusts, but the present writers have also given their observations concerning lithological characters of Łukowa beds.

Fragments of limestone beds with burrows of enteropneusts are housed at the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw, where they have been given catalogue numbers of Z. Pal. V. III/1-15.

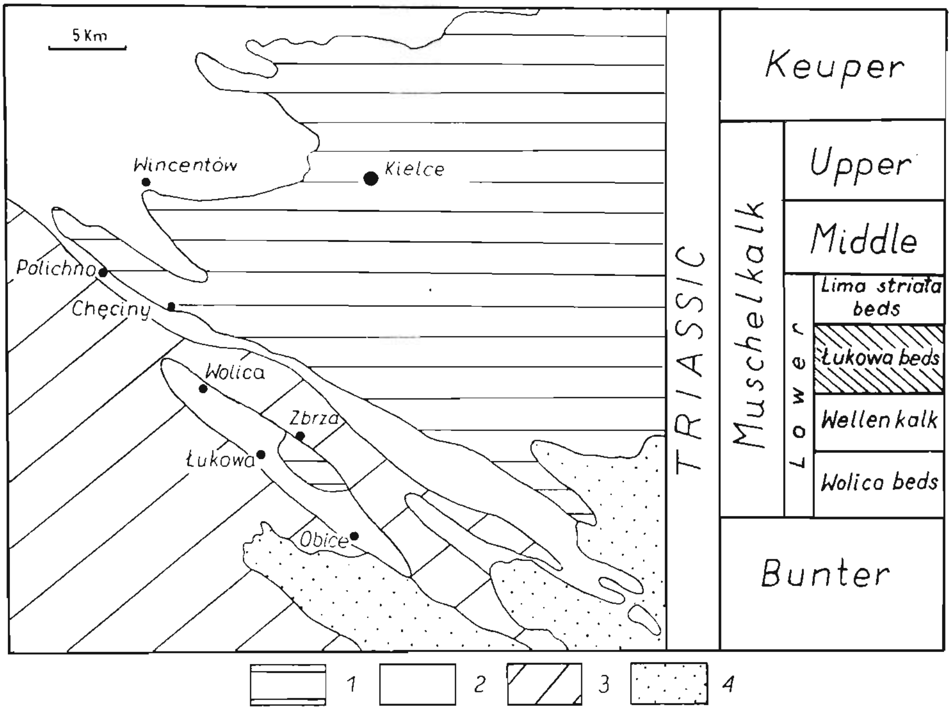

Fig. 1. — Location map and diagram of the stratigraphic division of the Triassic of the south-western Mesozoic border of the Holy Cross Mountains: *1* pre-Triassic deposits, *2* Triassic, *3* Jurassic and Cretaceous, *4* Miocene.

Except for Text-figs. 1 and 2, all photographs and drawings have been prepared by the first author.

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LITHOLOGICAL FEATURES OF ŁUKOWA BEDS

On the entire area under study, Łukowa beds are represented by gray, layered limestones about 30 m in total thickness. Here and there, they contain cherts and reveal the presence of sedimentary structures such as bedding, lamination and slump deformations (Text-fig. 2). Descriptions of general lithological characters may be found in Senkowiczowa's works (1957, 1959, 1961). Only brief petrological character of the complex with burrows of enteropneusts is given below.

Types of limestones

Within limits of Łukowa beds, the most common are, according to Folk's terminology (1959), micritic limestones, as well as biopelmicrites and biosparites, whereas pelsparites and intrasparites are less frequent. Finely grain-sized components predominate in the limestones of these types which, consequently, may be called calcilutites and calcarenites. Medium calcarenites are relatively frequent, whereas coarse calcarenites and calcirudites occur sporadically and in the form of thin layers.

A poor fauna of Łukowa beds is represented almost exclusively by pelecypods, gastropods and crinoids, gathered in thin layers. As most frequent genera of the groups referred to above, we may cite after Senkowiczowa (1957, 1959): *Lima, Pecten, Omphaloptycha, Undularia, Encrinus* and *Dadocrinus*. Fragmentary crinoids and valves of pelecypods make up essential components of the limestones of the types mentioned above, primarily of biosparites.

Sedimentary structures

Limestones of Łukowa beds are, in many cases, horizontally and diagonally bedded or laminated (Text-fig. 2). Bedding, frequently very delicate and visible only on weathered surfaces, occurs mostly in calcarenites of various types. The thickness of beds, which display stratification, fluctuates within limits of a few cm to 2 m, on the average amounting to several scores of cm. A horizontal or subhorizontal bedding is more frequent than cross-bedding and mostly occurs in the lower part of Łukowa beds. An upward decrease in grain-size of sediment is frequently observed in beds which display horizontal or low-angle cross-stratification. Bedding may reveal local slide and slump deformations which, in extreme instances, is manifested by the occurrence of fragments of beds torn apart or even of kneaded balls.

Also frequent are intraclasts to some dozen or so cm in size and usually displaying traces of mechanical reworking. They occur in thin layers, arranged with their longer axes parallel to the surface of stratification or bedding. The flattening and, in many cases, no sharp outlines are characteristic features of these intraclasts.

Rhythmical intercalations of micritic limestones and calcarenites (Text-fig. 2) are observed within the Łukowa beds, in particular in their upper part. The top of the micritic limestone usually represents an erosive, sharply outlined, even or uneven surface. Further up, there is usually an accumulation of coarser components (remains of fauna or intraclasts) of an overlaying sediment which upwards pass into a fine-grained sediment. There are also other sequences in which the difference in fraction of sediments is small and only different colouration of the rocks reveals the presence of a lithological contact erosive in character. With these contacts are usually connected the burrows of enteropneusts, which occur in greatest numbers in the higher part of Łukowa beds. Particular burrow horizons may be traced in quarries and in several successive outcrops,

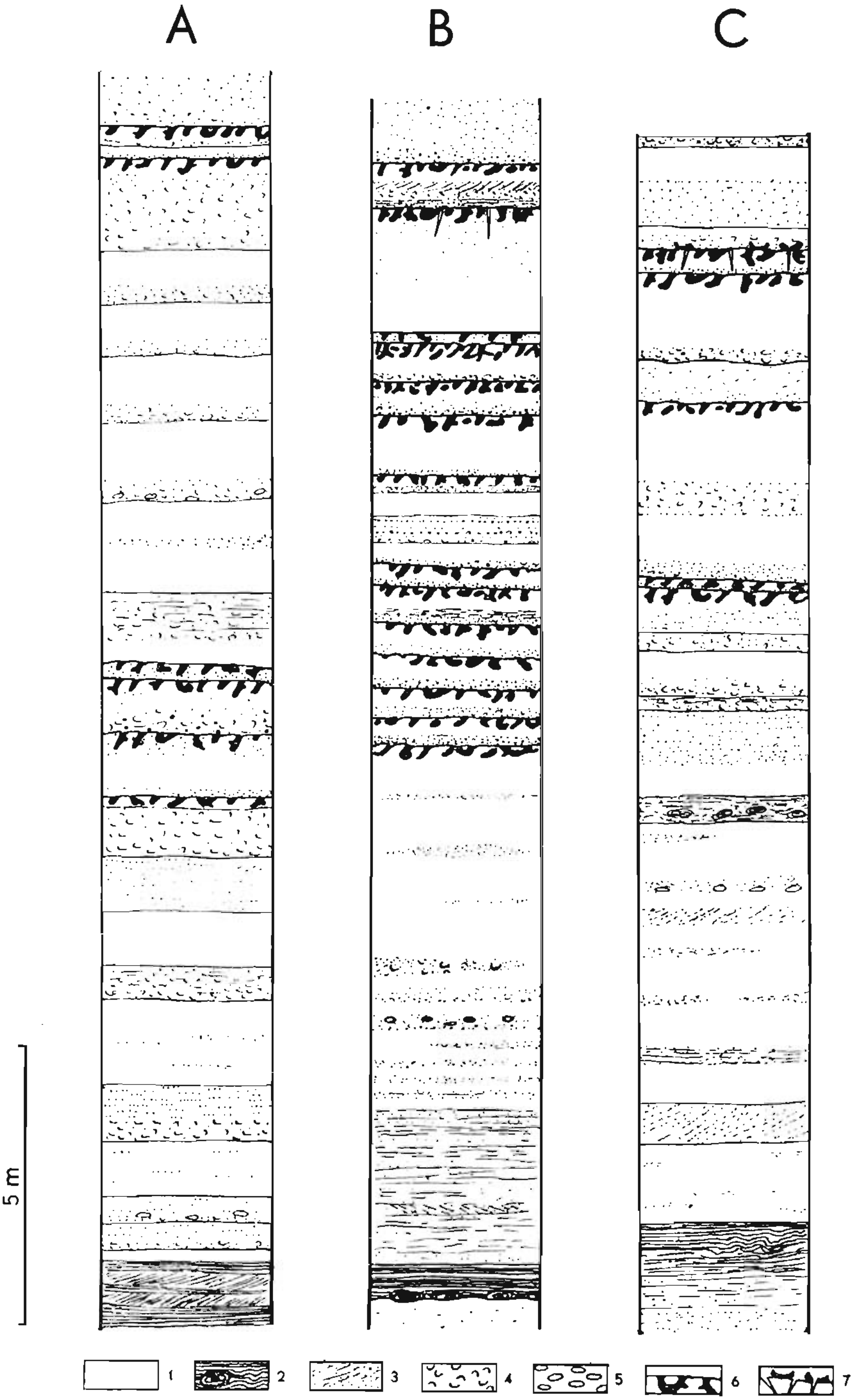

Fig. 2. — Lithological profiles of Łukowa beds of Muschelkalk: *A* Wincentów, *B* Polichno, *C* Wolica; *1* micritic limestones, *2* laminated limestones, in some cases with slide and slump deformations, *3* calcarenites, here and there cross-bedded, *4* coarser biocalcarenites, *5* larger intraclasts, *6* burrows of enteropneusts, *7* borings of the *Trypanites* type and oysters on the surface of beds bearing the character of „hard bottom".

but it is impossible to correlate them at great distances. In the profiles under study, the number of burrow horizons is varying (Text-fig. 2). Frequently, they disappear as a result of lateral facies changes.

MORPHOLOGY OF THE BURROWS

The burrows examined represent systems with a complex spatial configuration and on the whole consisting of horizontal segments, from which vertical or somewhat oblique segments, in some cases additionally bifurcated in their upper part, branch off towards the top of a bed (Text-fig. 3; Pl. IV, Figs. 2 and 3; Pl. V, Figs. 1 and 2). A burrow system consists, therefore, of several U-shaped tunnels connected with each other by horizontal branches (Text-fig. 4). Due to such connections, the burrow system of a single individual has many outlets on the surface of the bed. Usually, the outlets are irregularly distributed and, less frequently, arranged in double rows (Pl. III, Fig. 1; Pl. III, Fig. 3). Frequently, an outlet larger in diameter is surrounded by a few smaller ones. Larger outlets are round, oval, or sometimes, reniform in outline, smaller — only round. In longitudinal section, larger outlets are funnel-like (Text-figs. 3 and 4; Pl. III, Fig. 2), whereas smaller are straight tubes, their diameters equalling those of burrows or being somewhat smaller. Outlets of some burrows are situated on markedly elevated parts of a bed. Diameters of funnellike outlets reach 4.0 cm and of straight ones — 1.5 cm. The number of burrow outlets per unit of area comes to 15/100 sq cm of bed surface.

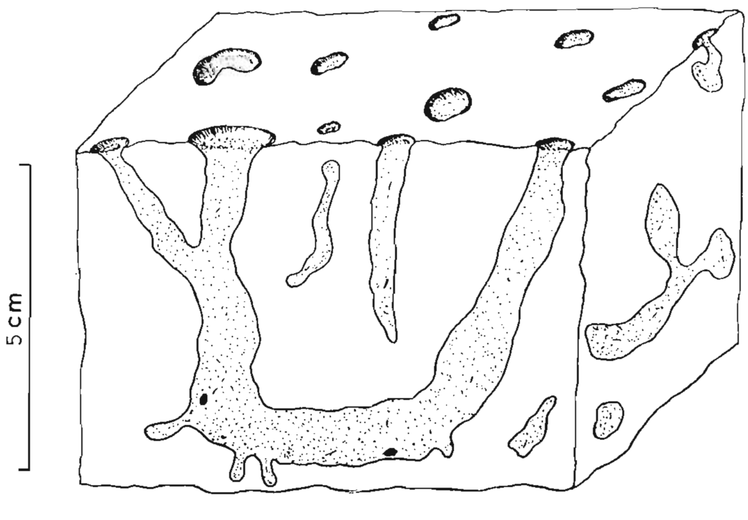

Fig. 3. — Spatial arrangement of a fragment of a burrow system of Triassic enteropneusts. The figure is drawn on the basis of a block cut out from a bed of micritic limestone with burrows (V.III/3). Hutka Hill at Polichno, Lower Muschelkalk (Łukowa beds).

In longitudinal sections the burrows are irregular, frequently bent and changing direction over short stretches. In transverse section, burrows are usually ellipsoid in outline with diameters varying within limits of 1.0 and 2.5 cm. Burrows, which were probably left by younger forms, are identical in morphology with the mentioned above, but with correspondingly smaller diameters of their transverse sections (within limits of 0.5 and 1.0 cm) occur in the same bed.

The presence of short, blind side-branchings is a characteristic feature of the burrows. Most frequently, they are oblique to the main burrow or, sometimes, they make up its blind end (Text-figs. 3 and 4; Pl. IV, Fig. 1; Pl. V, Fig. 2). Side-branchings are shaped like an irregularly outlined pear with a necklike contraction on the boundary with the main burrow. A bulblike swelling usually occurs at the end of such a branching. Some of them have a few swellings distributed along their trace. The length of the blind branchings amounts to 1—3 cm. The more strongly swollen, the shorter they are.

Despite the application of serial sections through large fragments of beds with burrows, a complete spatial reconstruction of a burrow system built by a single individual turned out to be impossible.

The lime sediment is penetrated by the burrows to own average depth of 10—15 cm from the surface of the bed. In many beds, however, the penetration depth is much smaller and does not exceed a few cm which should be ascribed to a strong erosion of the upper surface of the bed. In some cases, the extent of erosion is so great that horizontal sections of burrows occur on the surface of the bed in the form of a network of irregular, tortuous grooves.

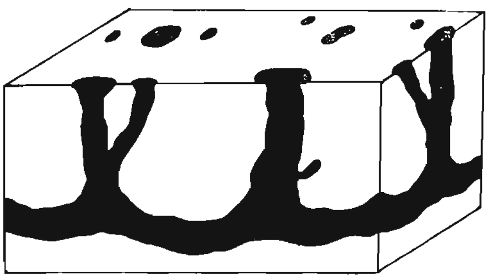

Fig. 4. — Spatial reconstruction of a burrow-system of the Triassic enteropneusts from the Holy Cross Mountains composed on the basis of serial sections of fragments of beds with burrows.

The boundary between a burrow and a sediment which surrounds it is usually very sharply outlined and the walls of only few burrows are blurred while the burrows themselves are irregularly deformed or flattened. In some cases, in the zone in which burrows contact the micritic sediment surrounding them, there occurs a dark, irregular envelope varying in thickness from a few mm to one cm and, outside the burrow, gradually passing into a common sediment light-gray in colour (Pl. III, Fig. 2; Pl. IV, Figs. 1-3; Pl. V, Figs. 1-3). In the case of burrows occurring in strongly marly limestones, the zone of change in the colouration of the sediment near the burrows is not marked.

Most burrows are filled with the micritic sediment sometimes with an admixture of calcarenite with rare intraclasts and a lumachelle detritus. The filling sediment is yellowish-white and in all cases, lighter in colouration than the surrounding sediment of the parent bed. In some burrows, aggregate assemblages of a coarse-sparry calcite, occur in addition to the filling sediment. Furthermore, some burrows are filled only with a sparry, yellow calcite. Empty burrow systems are observed in some of the beds. It is difficult to determine whether such burrows remained empty after they had been abandoned by the animals inhabiting them or the filling was secondarily washed out of them. The last-named possibility seems to be more likely, in particular if we take into account a considerable extent of karst processes in the Triassic limestones of the Holy Cross Mts. Likewise, it was probably the effect of karstic waters that led to the remodelling and extension of some now empty burrows, on the walls of which delicate, longitudinal grooves were left. This ornamentation does not seem to have anything in common with the original character of the burrow walls.

COMPARISON WITH OTHER BURROWS OF FOSSIL ENTEROPNEUSTA

In the palaeontological literature, there are only few mentions of the possibility of an enteropneust origin of some burrows. A small interest of palaeontologists in this problem may be explained, on the one hand, by a rarity of findings and difficulty of identification in a poorly preserved material and, on the other, by an until recently poor knowledge of the morphology and burrowing mechanism of Recent enteropneusts. The only mentions, suggesting the enteropneust character of some fossil burrows, concern also Middle Triassic German facies. Soergel (1923) called attention to the fact that U-shaped burrows with irregular side--branchings, which occur in Middle Triassic (Muschelkalk) limestones of Thuringia, are similar to those of Recent *Balanoglossus*. Similar burrows were also described by Mägdefrau (1932) from the lower part of the Muschelkalk of the environs of Jena. Burrows with funnellike outlets were called by the latter author *Balanoglossites triadicus*, and those otherwise identical with them but with outlets devoid of funnels — *Balanoglossites eurystomus*. In the same work Mägdefrau ascertained that the burrows he described were identical with those mentioned by Soergel (1923). Suggesting the enteropneust origin of the last-named burrows, Mägdefrau does not preclude the possibility of the participation of polychaetes in their formation.

In their general shape, burrows found by the present writers in Łukowa beds of Muschelkalk of the Holy Cross Mountains, are very similar to those described by Mägdefrau (1932), but a fragmentary and a rather poor preservation of the material illustrated by this author prevent both types of biostructures from being unequivocally identified. In comparing them with the Triassic material from the Holy Cross Mountains, Mägdefrau's separation of two different forms, based on the lack of funnellike outlets in some burrows, seems to be ill-founded. The lack of such outlets was most likely caused, as in the burrows from the Holy Cross Mountains, by the erosion of the bed surface. The present writers deliberately give up naming the burrows described, instead focussing their attention on collecting sufficient proofs for the enteropneust character of the burrows examined and showing their suitability to reconstruct their life time environment.

MECHANISM OF BURROWING IN RECENT ENTEROPNEUSTA

Studies on the mechanism of burrowing in Recent enteropneusts (Ritter, 1902; Brambell & Cole, 1939; Knight-Jones, 1952; Burdon-Jones, 1962) have shown that these animals are excellently adapted to the burrowing habit in a sediment. A muscular, wedgelike proboscis with a capability of a manipulation in a sediment with a considerable degree of firmness, is the main organ of movement. The penetration of the proboscis into the sediment is facilitated by a wavy movement of bulges caused by peristal-

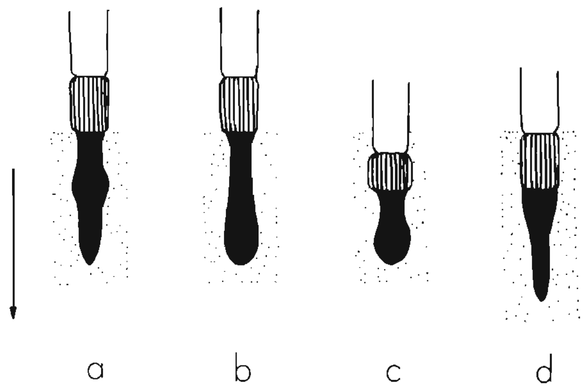

Fig. 5. — Diagram of the main stages of proboscis movement of Recent enteropneusts in the sediment (according to the descriptions of Ritter, 1902 and Knight-Jones, 1952): *a* squeezing the proboscis into the sediment by means of peristaltic contractions of circular muscles; *b* the formation of a bulge at the end of the proboscis as an instrument of a temporary anchorage in the sediment; *c* the contraction of the longitudinal muscles of the proboscis and collar and shifting the body for a small distance forward, *d* the next stage of sqeezing the proboscis into the sediment by means of peristaltic contractions of circular muscles.

tic contractions of circular muscles and running over its entire length (Text-fig. 5*a*). After a complete squeezing of the proboscis into the sediment, a prominent bulge, serving as a temporary anchorage of the animal in the sediment, is formed at the end of the proboscis (Text-fig. 5*b*) and thereafter, following a sudden contraction of longitudinal muscles of the proboscis and collar, the entire body moves forward for a short distance (Text-fig. 5*c*). Particles of sediment closely adjoining the proboscis are moved backwards by a strong water current, evoked by the movement of cilia densely lining the epidermis of the proboscis. Considerable part of sediment removed during burrowing passes through the alimentary canal and indigested mineral parts are periodically evacuated through the aims and, in the form of spiral castings, are deposited on the bottom surface. Thus, the burrowing enteropneusts eat out rather than burrow their tunnels (Van der Horst, 1940). Forms, which penetrate loose detrital sediments, secrete from the cells of epidermis on the proboscis and collar considerable amounts of mucus with which they cement the walls of burrows, thus assuring their durability and, at the same time, smoothness. The shape of the proboscis and primarily its length are characters which testify to the agility of enteropneusts in the sediment. Van der Horst (1940) noticed that *Balanoglossus studiosorum* Van der Horst, having a short, blunt proboscis is much less mobile in the sediment than the concurring *Balanoglossus hydrocephalus* Van der Horst having a long, pointed proboscis. The mobility of the proboscis is increased in some forms (e.g., *Saccoglossus pussilus* Ritter) due to the presence of a flexible neck with which it is attached to the collar. Such neck facilitates burrowing when the proboscis is strongly deflected from the axis of the body.

Burrowing enteropneusts display a considerable tolerance towards the grain-size of the sediment in which they live and they abound in sands, silty sands, silts as well as lime muds. It has been confirmed by the observations made in aquaria that the depth of burrowing in the sediment depends not only on the length of a given animal, but also on the thickness of the layer of sediment with an appropriate content of organic matter and on appropriate conditions of respiration in sediment (Burdon-Jones, 1962).

COMPARISON WITH MODERN BURROWS OF ENTEROPNEUSTA

Burrow systems of Triassic enteropneusts served, on the one hand, as a permanent shelter for their naked bodies and, on the other, sediment was — much the same as in Recent forms — an almost only source of nourishment, ingested in the form of fine organic remains and bacteria. Despite the abundance of enteropneusts in the intertidal zone accessible to direct observations, relatively few data on the spatial morphology of their burrows are given by the zoological literature. It results, however, from the studies on this subject, made so far (Stiasny, 1910; Brambell & Cole, 1939; Knight-Jones, 1953; Burdon-Jones, 1962), that, like Triassic forms, they construct multi-outlet burrow systems consisting of irregularly bent, interconnected, U-shaped tunnels. Like in Recent enteropneusts, some outlets of burrows of Triassic enteropneusts terminate in a funnellike depression, which (by analogy to the burrows of Recent enteropneusts) was probably formed as a result of a periodical thrusting out of the proboscis from the burrow and sweeping with it of the nearest environs of the burrow. Like in Recent forms, oblique side-branchings bifurcate from the upper part of the main burrow and open up on the surface of the bed in the form of funnellike outlets. The animal might have a few anal outlets which were distributed, like in Recent forms, around the outlet of the main burrow (Stiasny, 1910). It should be emphasized that the burrow systems of Recent enteropneusts frequently display considerable deviations from the structure plan presented above. In some Recent enteropneusts, the spatial orientation is quite irregular. The species are known which, in the anal part, have an irregularly spiral burrow system (Van der Horst, 1934, 1940).

Casts of proboscides preserved in the blind ends of side-burrows (Text-fig. 6*B*) make up a morphological character of Triassic burrows, enabling an unequivocal determination of the enteropneust origin of the burrows under study. The impression of the shape of a proboscis could

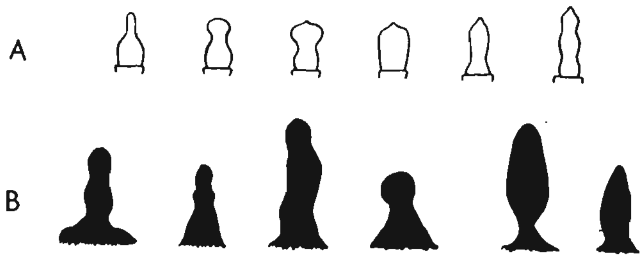

Fig. 6. — *A* different shapes of the proboscis of a Recent enteropneust during the movement (according to Van der Horst, 1940); *B* casts of proboscides of Triassic enteropneusts corresponding to different phases of manipulating this organ in the sediment. Drawings made from specimens coming from Łukowa beds of Polichno and Wolica; × 1.

be preserved only in the case when the animal withdrew for an indeterminate reason from its previous way of burrowing and did not return to it. The morphology of the casts of a proboscis has shown that various phases of the burrowing process, comparable with the phases of manipulating the proboscis in the sediment by Recent enteropneusts (Text-figs. 6 *A*, *B*) were fixed in such casts. The casts of proboscides withdrawn from the sediment in different stages of burrowing allow one to suppose that this organ in Triassic forms fulfilled, like in Recent enteropneusts, a fundamental locomotor function. A bare dozen or so of proboscis moulds have been found in the material examined, which was perfectly understandable since under normal conditions the animal continued burrowing until it reached the surface of sediment.

The dimensions of the moulds of proboscides and the lengths of U-shaped tunnels enabled an approximate determination of the dimensions of the forms which burrowed these tunnels. Thus, an approximate length of adult Triassic enteropneusts should amount on the average to 15—20 and of their proboscides — to 1.5—2.0 cm. These magnitudes are similar to average dimensions of most of Recent forms (Hyman, 1959).

Darker envelopes, which occur in the zone of contact between burrows and sediment, may be interpreted as a change in colouration of the sediment caused by the mucus secreted, as in Recent forms, during burrowing. Similar darker envelopes caused by mucus were observed near the burrows of Recent burrowing Crustacea (Shinn, 1968). Like in Recent enteropneusts, the walls of Triassic forms are completely smooth, without any traces of ornamentation.

ANALYSIS OF PALAEOECOLOGICAL CONDITIONS

Substratum

It is clear from the lithological profiles of Łukowa beds (Text-fig. 2) that the burrows of enteropneusts occur in micritic and fine-grained sediments and only rarely in calcarenites. The settlement of micritic sediments was primarily related to a sufficient organic matter content taken in by the enteropneusts directly from the sediment. Burrow horizons outcropped in a quarry at Wolica (Pl. I), in which burrows of enteropneusts occur only in a sediment zone with a markedly darker colouration, may serve as an example of a selective adoption of the sediment as a substratum. Among other factors, a certain role in the nutrition of enteropneusts might be played by the accumulation of faecal pellets, observed by the present writers in thin sections. As a result of washing and sorting of the sediment, the content of organic remains of calcarenites was less abundant. In many cases, a marked avoidance and bypassing by enteropneusts of more detrital parts of sediment within the bed (Text-fig. 8) was observed. A similar phenomenon was also recorded in the cases in which the detrital sediment occurred in the underlaying layer (Text-fig. 7). These observations are in conformity with the correlations that occur between the content of organic remains of the sediment and the density of population of Recent enteropneusts, for instance, *Saccoglossus apatensis* Thomas, which occurs on the coasts of South Australia, densely settles dark-silty muds filling pits in granite and which is only rarely found in adjoining sands (Thomas, 1956).

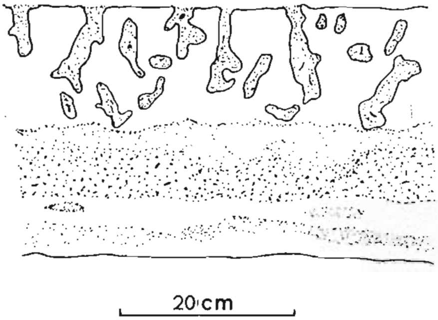

Fig. 7

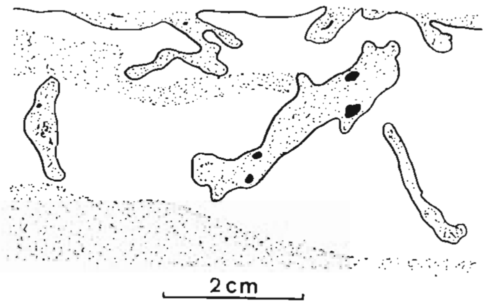

Fig. 8

Fig. 7. — Transverse section through a bed of micritic limestone with burrows of enteropneusts. The depth of penetration of the burrows is limited only to the micritic limestone; the burrows avoid the detrital underlying layer. A quarry at Wolica, Lower Muschelkalk (Łukowa beds).

Fig. 8. — Transverse section through the fragment of a bed of micritic limestone with burrows of enteropneusts. The burrows avoid the detrital intercalations in the micritic sediment. The older generation of the burrows is strongly eroded and remodelled. A quarry at Wincentów, Lower Muschelkalk (Łukowa beds).

The consolidation of lime mud during the life time of enteropneusts could not be far advanced since, if such would be the case, the manipulation with a proboscis devoid of skeletal elements would be impossible for those animals. The consistence of the sediment was probably semi-plastic which is confirmed by distinct traces of deformation of some burrows and by the blurred boundaries between burrows and the sediment. Dark, irregular envelopes in the places in which burrows contacted the surrounding sediment (Pl. IV, Figs. 1-3; Pl. V, Figs. 1-3) are also indicative of a relatively soft consistence of the bottom sediment. The irregular occurrence of the envelopes might indicate that only looser parts of sediment required hardening by the animal. In Recent enteropneusts, the looser the sediment, the more intensive is the secretion of mucus (Knight-Jones, 1953; Burdon-Jones, 1962).

The settlement of the bottom by Triassic enteropneusts could take place only under the conditions of a delayed or retarded deposition. In the light of the actuopalaeontological studies, such conditions are necessary for the life in sediments of all burrowing and boring forms (Reineck, 1958; Schäfer, 1962; Goldring, 1964 and others). An increase in the deposition resulted in burying burrows, made respiration difficult and led to the migration of enteropneusts from the settled area. On the other hand, a longer period of slighter deposition or non-deposition might, in some cases, lead to a relative hardening of the superficial zone of sediment and also arrest the development of enteropneusts. In such cases, the surface of the bottom was occupied by boring and encrusting organisms. Thin borings of the *Trypanites* Mägdefrau type (Text-fig. 9; Pl. IV, Fig. 1) were an only boring form recorded by the present writers in Łukowa beds (Wolica and Polichno profiles, Text-fig. 2) and which concurred with strongly abraded burrows of enteropneusts. These forms are identical with borings described, also from Muschelkalk, from Southern Germany (Mägdefrau, 1932; Müller, 1956). Together with borings of the *Trypanites* type, here and there occur small oysters (*Ostrea* sp.), attached to the surface of the bottom and sometimes bored by *Trypanites* (Text-fig. 9). The concurrence of burrowing, boring and encrusting forms is

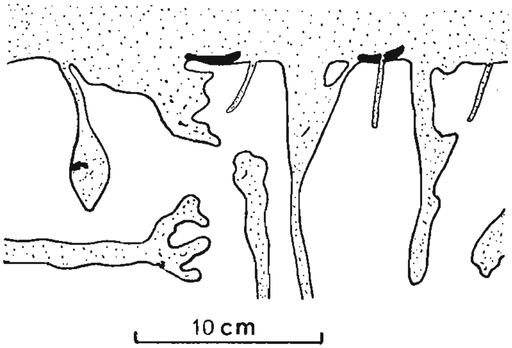

Fig. 9. — Transverse section through the fragment of a bed of micritic limestone with burrows of enteropneusts. The parts of burrows near the surface of the bed and the outlets are erosively remodelled and extended. The top surface of the bed, encrusted by small oysters and bored by the *Trypanites* type borings, bears the character of a „hard bottom". A quarry at Wolica, Lower Muschelkalk (Łukowa beds).

a symptom of the succession of biocoenoses, related to a gradual change in the consolidation of the bottom sediment, during the break in sedimentation, progressively from the „soft" to the „hard" stage (Kaźmierczak & Pszczółkowski, 1968). As results from the present writers' observations, the „hard" bottom stage was, however, relatively infrequently reached within the limits of Łukowa beds.

Bathymetry

As results from the studies on Recent burrowing enteropneusts, their occurrence is recorded almost exclusively in the lowermost part of the intertidal zone and only rarely — somewhat below it (Barrington, 1965). As regards the forms get from larger depths, no information on their mode of life in sediment is available so far. At any rate, an abundant occurrence of enteropneusts is related only to the zone included in the direct activity of tidal currents.

The abundance of burrows of enteropneusts in the Triassic (Muschelkalk) of the Holy Cross Mountains suggests that the bathymetric conditions during the deposition of Łukowa beds were probably similar to those observed of nowadays. Similar conclusions may be drawn from the analysis of the sediments in which these burrows occur. A relatively high content of the pelletoid sediments, as well as biosparites and intrasparites of Łukowa beds is a characteristic feature of the formations of the inter- and subtidal zones on the recent and fossil areas of the carbonate sedimentation (Roehl, 1967). Similar sediments are also met with in the inter- and subtidal zones of the areas of a recent silt and sandy deposition (Reineck, 1958*a*; Van Straaten, 1959; Reineck, Gutmann & Hertweck, 1967). Such sedimentary structures as a horizontal and cross-lamination and cross-stratification are also indicative of an extremely shallow-water sedimentation (comp. Van Straaten, 1959; Masters, 1967 and others). Large intraclasts, very often recorded in Łukowa beds (comp. also Senkowiczowa, 1961), are comparable with „flat pebbles", whose genesis is usually related to so shallow environment (Gripp, 1956; Ginsburg, 1957; Roehl, 1967) that, in the case under study, it is reasonable to assume that they were redeposited in a slightly deeper zone.

To sum up, the presence of the burrows of enteropneusts in the Lower Muschelkalk sediments should be related to a very shallow environment fluctuating within limits of the uppermost part of the subtidal, and the lowermost part — of the intertidal zones.

Hydrodynamic activity

Despite a considerably shallow water, the hydrodynamic activity of the environment settled by enteropneusts was on the whole not great. The fact that the burrows are preserved in the beds some dozen or so cm in thickness (Text-fig 2), is a direct proof for this phenomenon. With the low degree of consolidation of the lime mud, in which enteropneusts sought food, a very strong movement of the water was bound to lead to a rapid destruction of the layer containing burrows. Most surfaces of beds with burrows bear the traces of erosion represented by the remodelling of the outlet parts of burrows and inequalities of the top surface which, in some cases, reach a dozen or so cm. Some burrows are abraded to 3/4 of their original height (Text-fig. 8). On the other hand, no erosional channels, deeply indented in bottom sediments, are observed. Hence, we may assume that the sediments were subject to a relatively small, although permanent, erosion which elucidates the fact that the burrows of enteropneusts with preserved funnellike outlet occur rarely. The preservation of such outlets in fossil state testifies to the fact that the bottom was rapidly covered with a detrital sediment.

The types of the sediments in which the burrows of Triassic enteropneusts occur are indicative of an environment with a moderate turbulence (comp. Bissel & Chillingar, 1967). Horizontal and low-angle cross-stratifications, are predominant types of bedding.

A rhythmic interbedding of sediments, varying in grain-size and frequently separated from each other by erosional surfaces (Text-fig. 2) should be ascribed to the periods of a stronger turbulence occurring in this part of the sedimentary basin, for instance, repeated storm seasons during which successive populations of enteropneusts might be destroyed. Phenomena of such type are common on flat intertidal areas settled by burrowing animals (Reineck, 1958*a*,*b*; Schäfer, 1962; Reineck, Gutmann & Hertweck, 1967 and others). In the time of a stronger turbulence the biodetrital layers were deposited, probably as a result of the reworking of the superficial sediments.

PALAEOGEOGRAPHICAL REMARKS

The suggested sedimentary environment of Łukowa beds, in which the burrowing enteropneusts lived, is in conformity with a general palaeogeographical schema adopted so far for this part of the Lower Muschelkalk basin (Senkowiczowa, 1961). The coasts of the nearest emerged area were situated north-east of the Holy Cross region (Senkowiczowa, 1963). The deposition of Łukowa beds took place on the shoals affected by the activity of tidal currents, which in this area were rather weak because their force was damped on flat, extensive areas of the shelf. The Thetis should be considered a source zone of the tides. Abundant enteropneusts, distributed over limited areas of the bottom depending on local bathymetry and type of the bottom sediment, lived under such conditions. Such an occurrence range of these animals explains a relatively small extent of particular burrow horizons of enteropneusts in Łukowa beds.

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JÓZEF KAŹMIERCZAK & ANDRZEJ PSZCZÓŁKOWSKI

KANAŁY JELITODYSZNYCH (ENTEROPNEUSTA) W WAPIENIU MUSZLOWYM GÓR ŚWIĘTOKRZYSKICH

Streszczenie

Przedstawiono wyniki badań nad kanałami organizmów ryjących, występujących masowo w osadach dolnego wapienia muszlowego południowego i zachodniego obrzeżenia mezozoicznego Gór Świętokrzyskich. Autorzy dowodzą, że kanały te powstały w wyniku ryjącej działalności jelitodysznych (Enteropneusta).

Jelitodyszne triasowe, podobnie jak większość dzisiejszych form ryjących, tworzyły systemy wielowylotowych kanałów złożonych z nieregularnie powyginanych, połączonych ze sobą U-kształtnych tuneli. Wyloty części kanałów, podobnie jak u form dzisiejszych, zakończone są lejkowatymi zagłębieniami. Od kanału głównego odchodzą w części górnej ukośne kanały boczne, również o wylotach lejkowatych. Dookoła wylotów lejkowatych występuje niekiedy kilka mniejszych wylotów, które odpowiadałyby wylotom analnym przez analogię z systemami kanałów enteropneustów dzisiejszych.

Główną cechą morfologiczną opisanych kanałów, wskazującą na ich enteropneustowe pochodzenie, są zachowane niekiedy odlewy ryjków w ślepych zakończeniach kanałów bocznych. Kształty tych odlewów wskazują, że są to utrwalone różne fazy procesu rycia, porównywalne z fazami manewrowania ryjkiem w osadzie u enteropneustów dzisiejszych. Zachowane odlewy ryjków pozwalają przypuszczać, że organ ten u form triasowych pełnić musiał, jak u dzisiejszych, podstawową funkcję lokomotoryczną. Wymiary odlewów ryjków oraz pomierzone długości U-kształtnych kanałów pozwoliły w przybliżeniu określić rozmiary enteropneustów triasowych.

Ich długość wynosiła średnio 15—20 cm, przy długości ryjka 1,5—2,0 cm. Nieregularne, ciemne otoczki, występujące w strefie kontaktowej wielu kanałów z osadem, powstały przypuszczalnie w rezultacie wydzielania śluzu w trakcie rycia, cementującego ścianki kanałów. Ścianki kanałów, podobnie jak u form dzisiejszych, są gładkie, bez ornamentacji.

W całej dotychczasowej literaturze paleoichnologicznej kanały przypisywane enteropneustom wzmiankowane są jedynie z dolnego wapienia muszlowego południowych Niemiec (Mägdefrau, 1932). Kanały te ogólnym pokrojem zbliżone są bardzo do kanałów enteropneustów z Gór Świętokrzyskich, jednak pełne porównanie wymienionych biostruktur uniemożliwia niezbyt dobry stan zachowania i zilustrowania materiału niemieckiego.

Z profilów litologicznych warstw łukowskich wynika, że kanały enteropneustów występują głównie w osadach pelitowych, rzadko — drobnodetrytycznych. Taki selektywny dobór zasiedlanego podłoża związany był zapewne z odpowiednią zawartością substancji organicznych w osadzie, przetrawianych w trakcie rycia. Enteropneusty wyraźnie unikały przemytych wkładek detrytycznych w obrębie tej samej ławicy. Stopień skonsolidowania mułu wapiennego w czasie życia enteropneustów nie mógł być zbyt znaczny, ze względu na ograniczone możliwości operowania ryjkiem pozbawionym twardych elementów szkieletowych. Osad miał przypuszczalnie konsystencję półplastyczną, co potwierdzają wyraźne ślady zdeformowania niektórych kanałów. Zasiedlanie dna przez enteropneusty triasowe zachodziło w warunkach zwolnionej lub zahamowanej sedymentacji. Szybsze tworzenie się osadów powodowało zasypywanie kanałów i prowadziło do migracji enteropneustów z zasiedlanego obszaru. Dłuższy brak sedymentacji prowadził do względnego stwardnienia przydennej strefy osadu i również ograniczał działalność enteropneustów. Wówczas powierzchnia dna była zajmowana przez organizmy drążące i narastające (kanaliki typu *Trypanites* Mägdefrau, *Ostrea* sp.).

Obfitość kanałów enteropneustów w środkowym triasie Gór Świętokrzyskich pozwala sądzić, że warunki batymetryczne były w tym czasie bardzo zbliżone do tych, w jakich żyją dzisiejsze enteropneusty ryjące. Są one związane prawie wyłącznie z najniższą częścią strefy międzypływowej, rzadziej ze strefą subpływową. Na takie stosunki batymetryczne wskazuje również charakter facjalny osadów, w których występują zbadane kanały (osady z licznymi grudkami fekalnymi, osady biodetrytyczne, detrytyczne, warstwowania poziome i skośne, płaskie otoczaki, zaburzenia osuwiskowe). Pomimo znacznej płytkowodności, turbulencja środowiska, w jakim żyły enteropneusty, nie była zbyt wielka. Większość ławic z kanałami podlegała nieznacznej erozji, tylko w kilku przypadkach kanały ścięte są erozyjnie o 3/4 pierwotnej wysokości. Silniejsza erozja mogła mieć miejsce w czasie powtarzających się okresowo sztormów, niszczących kolejne populacje enteropneustów. Enteropneusty triasowe żyły masowo na ograniczonych powierzchniach dna, w zależności od lokalnej batymetrii i typu osadu. Znajduje to potwierdzenie w niewielkim zasięgu poszczególnych poziomów z kanałami w obrębie warstw łukowskich.

ЮЗЭФ КАЗЬМЕРЧАК И АНДЖЕЙ ПЩУЛКОВСКИ

ХОДЫ КИШЕЧНОДЫШАЩИХ (ENTEROPNEUSTA) В РАКОВИННОМ ИЗВЕСТНЯКЕ (MUSCHELKALK) СВЕНТОКШИСКИХ ГОР, ПОЛЬША

Резюме

В настоящей работе представлены результаты исследований ходов роющих организмов, находящихся в массовом количестве в нижней части раковинного известняка (луковские слои) южного и западного мезозойского обрамления Свентокшиских гор. Авторы доказали, что эти ходы возникли вследствие роющей деятельности кишечнодышащих (Enteropneusta).

Триасовые Enteropneusta, как и большинство современных роющих форм, оставляли системы многовыходных ходов, состоящих из неправильно изогнутых, соединенных между собой U-образных туннелей. Устья ходов, также как и у современных форм, имеют окончания в виде углублений, имеющих формы воронки. От главного хода в верхней части отходят косые боковые ходы с такими же окончаниями. Вокруг этих выходов иногда находится несколько меньших выходов, которые, аналогично системам ходов у современных Enteropneusta, могут соответствовать анальным устьям.

Основной морфологической чертой описанных ходов, свидетельствующей о их принадлежности кишечнодышащим, являются сохранившиеся в ряде случаев в слепых окончаниях ходов ответвления, имеющие форму хоботков. Форма этих ответвлений указывает на то, что это следы различных фаз процесса рытья, которые можно сравнивать с фазами маневрирования хоботком в осадке у современных Enteropneusta. Сохранившиеся следы хоботков позволяют предполагать, что этот орган у триасовых форм выполнял, как и у современных форм, основную локомоторную функцию. Размеры следов хоботков и измеренные длины U-образных ходов позволили приблизительно определить величину триасовых Enteropneusta. Их средняя длина была 15—20 см, при длине хоботка 1,5—2,0 см. Темные оболочки неправильной формы, присутствующие в некоторых случаях в контактной зоне осадка и хода, образовались вероятно в результате слизеотделения, цементирующего стенки ходов во время рытья. Эти стенки, так же как и у современных форм, гладкие, без скульптуры.

В существующей до сих пор палеоихнологической литературе ходы, относимые к Enteropneusta, известны только из нижней части раковинного известняка южной Германии (Mägdefrau, 1932). Эти ходы по внешнему виду очень похожи на ходы Enteropneusta из Свентокшиских гор, однако отождествление этих структур невозможно из-за плохой сохранности и малого количества иллюстраций в указанной работе.

В разрезах луковских слоев видно, что ходы Enteropneusta связаны главным образом с тонкозернистыми, реже с мелкодетритовыми осадками. Такой выбор субстрата вероятно был связан с количеством органического вещества

в осадке. Enteropneusta явно избегали промытых детритовых прослоек в пределах одной банки. Степень диагенеза известкового ила во время жизни Enteropneusta видимо была незначительной, так как хоботок не имеет твердых скелетных элементов и был неприспособлен к рытью в твердом субстрате. Осадок имел по всей вероятности полупластичную консистенцию, о чем свидетельствуют четкие следы деформации некоторых ходов. Заселение дна триасовыми Enteropneusta происходило в условиях замедленной или приостановленной седиментации. Более скорое осадкообразование вызывало засыпание ходов и было причиной миграции Enteropneusta из заселенного участка. Длительный перерыв в седиментации вызывал относительную консолидацию придонной зоны осадка и тем самым ограничивал деятельность Enteropneusta. Поверхность дна в это время заселяли сверлящие (сверления типа *Trypanites* Mägdefrau) и прикрепляющиеся организмы (*Ostrea* sp.).

Обилие ходов Enteropneusta в среднем триасе Свентокшиских гор позволяет говорить о том, что батиметрические условия в это время были близки к тем, в которых обитают современные роющие Enteropneusta. Они связаны почти исключительно с самой нижней частью полосы прилива и отлива, реже с зоной ниже полосы отлива. Об этом свидетельствует также фациальный характер осадков, в которых находятся изученные ходы (осадки с обильными фекальными комочками, биодетритовые и детритовые осадки, горизонтальная и косая слоистость, плоские гальки, оползневые нарушения). Несмотря на значительное мелководье, подвижность среды, в которой обитали Enteropneusta, не была значительной. Большинство банок с ходами подвергалось слабой эрозии и только в нескольких случаях ходы срезаны вследствие эрозии до размера равного примерно $^1/_4$ их первоначальной высоты. Более значительная эрозия могла происходить во время повторяющихся шквалов, которые уничтожали очередную популяцию Enteropneusta. Триасовые Enteropneusta в массовом количестве обитали на ограниченных участках дна, в зависимости от местных батиметрических условий и типа осадка. Это подтверждается невыдержанностью по простиранию отдельных горизонтов, вмещающих эти ходы в пределах луковских слоев.

PLATES

Plate I

Figs. 1-2. Transverse sections through a bed of micritic limestone with burrows of enteropneusts. The sediment, in which the burrows occur, is markedly darker than the under- and overlying sediment. A quarry at Wolica, Lower Muschelkalk (Łukowa beds); × 0.25.

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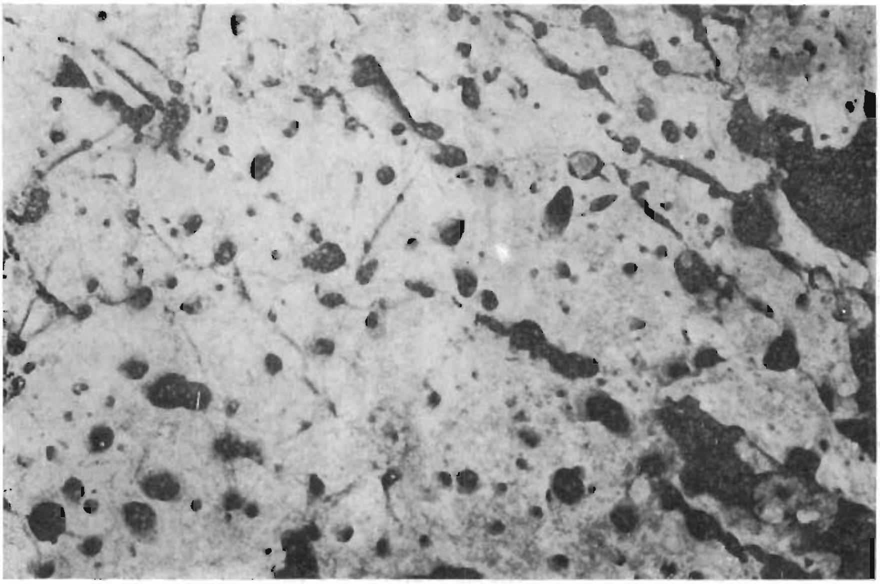

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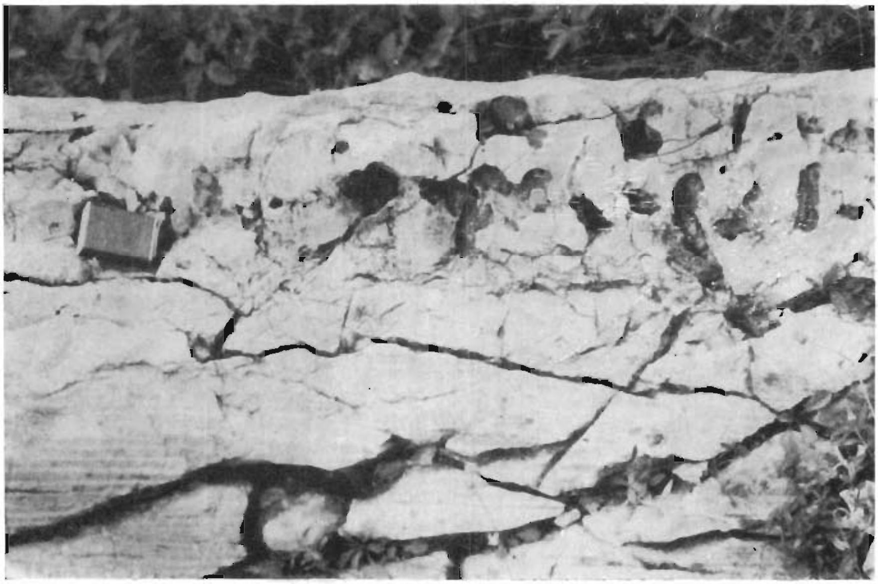

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Plate II

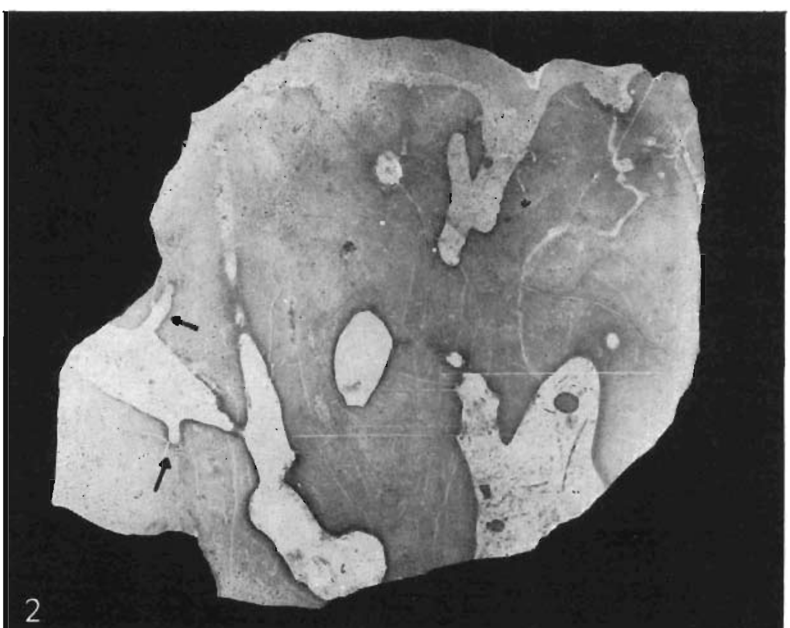
Fig. 1. Surface of a bed of micritic limestone with many outlets of burrows of enteropneusts. Smaller, anal outlets are visible around the erosively reworked outlets of main burrows. Hutna Hill at Polichno; Lower Muschelkalk (Łukowa beds); × 0.17.

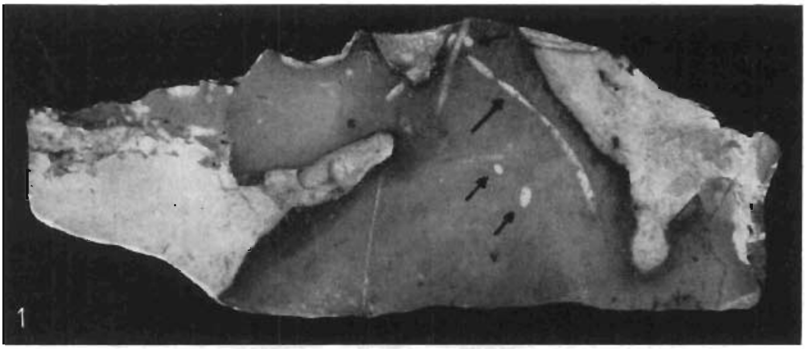
Fig. 2. A bed of micritic limestone with karstically extended burrow systems of enteropneusts, shown in transverse section. A horizontally bedded calcarenite makes up the underlying layer. Hutna Hill at Polichno; Lower Muschelkalk (Łukowa beds); × 0.17.

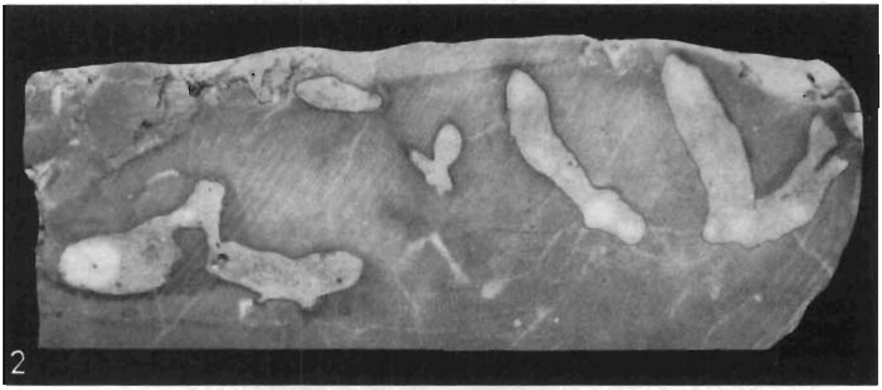
Plate III

Figs. 1-2. Two fragments of a bed of micritic limestone with burrows of enteropneusts. A funnellike outlet of a burrow on the surface of the bed and casts of proboscides of enteropneusts (marked with arrows) in blind ends of side — burrows are visible. In the zone of contact of burrows and the sediment thin, darker rims, formed by the saturation of the burrow wall with the cementing mucus, are visible (V.III/12—13). A quarry at Wolica, Lower Muschelkalk (Łukowa beds); × 0,75.

Fig. 3. A fragment of the surface of a bed with outlets of burrows of enteropneusts arranged in pairs. A funnellike outline of larger outlets (V.III/15) is visible. Łukowa, Lower Muschelkalk (Łukowa beds); nat. size.




1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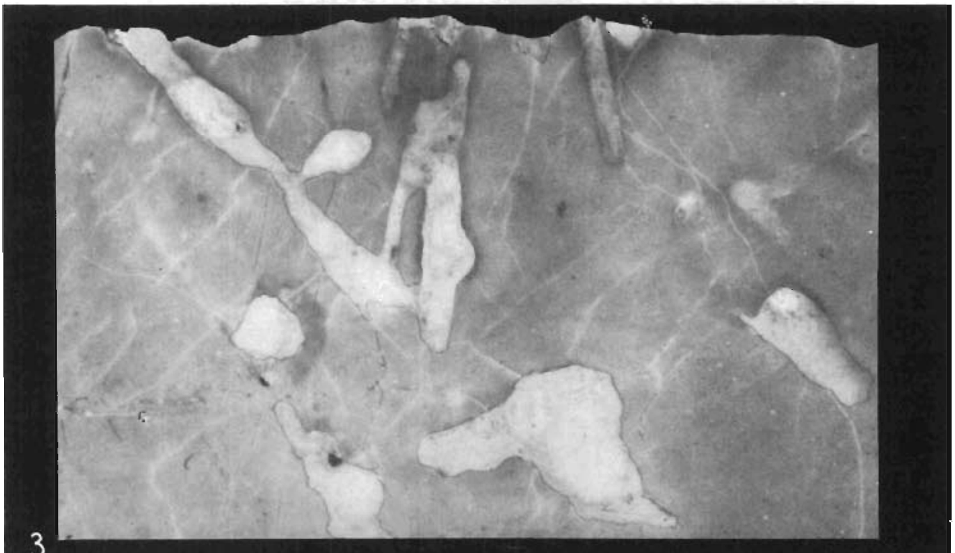
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Plate IV

Fig. 1. A fragment of a bed of micritic limestone with burrows of enteropneusts. Well preserved casts of proboscides in blind ends of side-burrows surrounded with a dark rim are visible. Thin borings of the *Trypanites* Mägdefrau type (marked with arrows) are revealed in the plane of section. The surface of the bed with distinct traces of erosion (V.III/11). A quarry at Wolica; Lower Muschelkalk (Łukowa beds); nat. size.

Fig. 2. Transverse section through another fragment of micritic limestone with burrows of enteropneusts. Some parts of horizontal and vertical sections of a burrow-system are visible on the left and a full U-shaped outline of a burrow (V.III/5) — on the right. Hutka Hill at Polichno, Lower Muschelkalk (Łukowa beds); × 0.8.

Fig. 3. Another fragment of a bed of micritic limestone with burrows of enteropneusts. *A* U-shaped outline of a burrow with a single side-burrow (V.III/3) is visible. Hutka Hill at Polichno, Lower Muschelkalk (Łukowa beds); × 0.8.

Plate V

Figs. 1-3. Three different transverse sections through a bed of micritic limestone with burrows of enteropneusts. Casts of proboscides in blind ends of side-burrows (V.III/1) are marked with arrows. An outline of the fragment of a burrow system consisting of two U-shaped tunnels (V.III/2) is visible in Fig. 1. The surface of the bed is strongly eroded, uneven. Hutka Hill at Polichno, Lower Muschelkalk (Łukowa beds), Figs. 1 and 3 × 0.8, Fig. 2 — nat. size.