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Sedimentological, Ecological and Temporal Patterns of Fossil Lagerstatten [and Discussion]

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Sedimentological, ecological and temporal patterns of fossil Lagerstätten

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[Plate 1]

Preservation of non-mineralized structures (including plants) and of articulated skeletons results from extraordinary hydrographic, sedimentational and early diagenetic conditions. The corresponding chief causative effects (stagnation, obrution and bacterial sealing) define a conceptual continuum into which individual occurrences may be mapped. A more pragmatic, typological classification of conservation deposits, using a standard questionnaire, reveals ecological replacements, as well as trends related to the evolution of the biosphere, through geological time.

The theme of this symposium, 'extraordinary fossil biotas: their evolutionary and ecological significance', recalls a project carried out some time ago in the Tübingen special research division 53 on palaeoecology. Our term 'fossil Lagerstätten' (alternative spelling: Lagerstaetten) is difficult to translate into English. Corresponding to economic Lagerstätten of minerals and ores, fossil Lagerstätten were defined as rock bodies unusually rich in palaeontological information, either in a quantitative or qualitative sense. This means that the term embraces not only strata with an unusual preservation, but also less spectacular deposits such as shell beds, bone beds and crinoidal limestones. The concept also implies that there is no sharp boundary with 'normal' fossiliferous rocks. Rather, the preservation of any fossil is to be considered as an unusual accident that deserves attention and questioning.

The rationale behind such a broad approach is a sedimentological one. Fossil Lagerstätten are considered as end members of ordinary sedimentary facies, in which the unusual amount and quality of the palaeontological test bodies allows us to identify better the factors responsible for such a facies at all levels of its genesis: biotope conditions (palaeobiology), fate of the soft parts and organic skeletal material (necrolysis), sedimentary transport and burial (biostratinomy) and fate of the mineralized skeletons (fossil diagenesis).

On the other hand this approach is based on the contention that in spite of all the possible combinations and variations of biotic and abiotic factors involved there is a finite number of situations that lead to the formation of fossil Lagerstätten and that prospecting for them is therefore a realistic objective. A first step in this direction was a genetic classification (figure 1), the broad outlines of which are still valid.

In the meantime, our understanding of *concentration deposits* has been greatly improved by the concepts of dynamic and event stratigraphy with far reaching applications in basin analysis (see Einsele & Seilacher (1982) and Bayer & Seilacher (1985) for examples and references).

With respect to *conservation deposits*, on which this symposium is focused, many new examples have been discovered and old ones analysed in more detail, including case histories presented in this symposium. Each of them has, of course, its merit as a peephole in the screen of imperfect

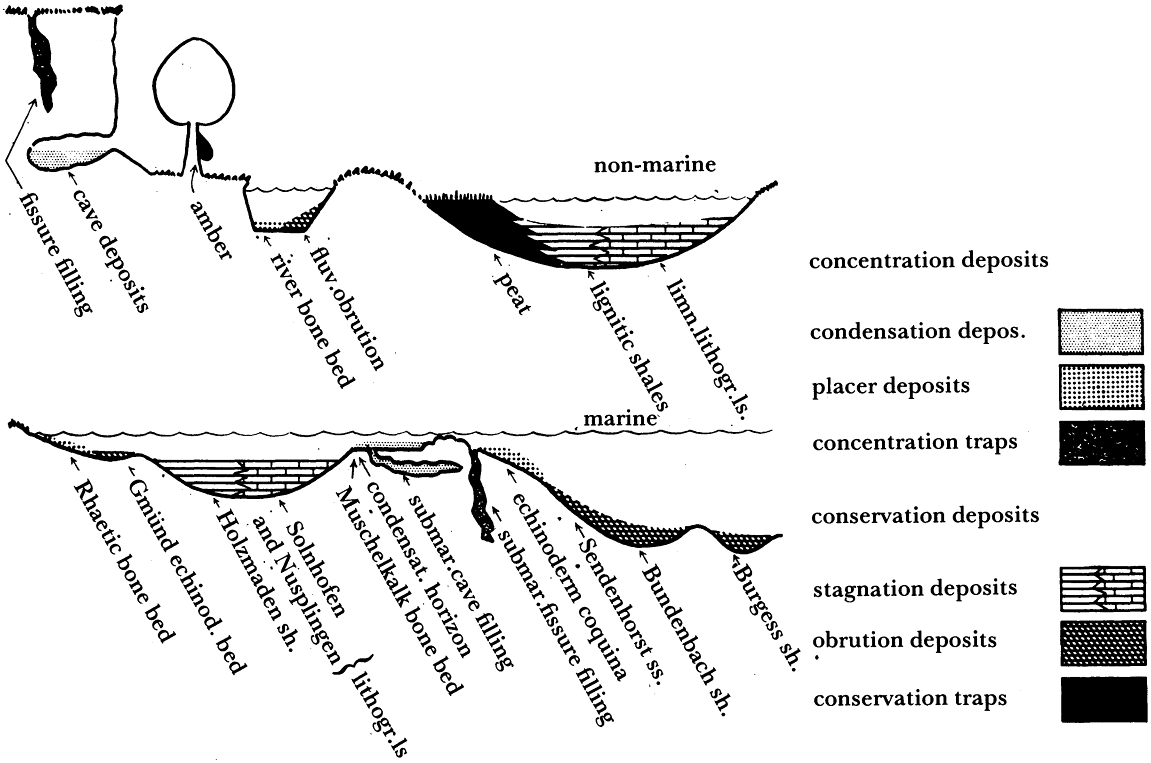

FIGURE 1. Synopsis and classification of fossil Lagerstätten as given by Seilacher & Westphal (1971).

preservation, through which we can see unknown anatomical details and new, commonly problematic taxa. But each case is also important as an additional test for environmental and diagenetic boundary conditions in our classification.

Instead of adding new examples, we shall here choose three well studied and representative examples from the Jurassic of southern Germany as a reference, and try to derive from them a questionnaire that can be applied to other conservation deposits.

In doing so, we shall emphasize the invertebrate rather than the vertebrate, microfossil and plant records, because invertebrates cover a wider spectrum with regard to geological time, biomaterials and environments.

1. The echinoderm Lagerstätte of Gmünd (L. Sinemurian): an obrution deposit

Being only a few centimetres thick and possibly no more than a few metres in lateral extent, this deposit can not compete with those of Holzmaden and Solnhofen. But its fossil content, the stratigraphic context and low level of genetic complexity as well as a careful analysis by Rosenkranz (1971) make it a very suitable prototype of what we call obrution deposits.

(a) *Stratigraphic situation*

Stratigraphically, the fossil-bearing lens of black shale is separated from contact with the underlying terrestrial Keuper marls by a conglomeratic shell bed 0.5–0.6 cm in thickness and overlain by a similar conglomeratic limestone. Palaeontological evidence, however, shows that this basal conglomerate of the Jurassic transgression represents in fact a rather complex environmental history.

The erosional nature of the Triassic–Jurassic contact is shown first by the absence of the Rhaetic, which in this area is usually represented by coal-bearing swamp deposits which pass into marine sands and clays farther to the west. Second, the conglomerate consists largely of reworked calcareous concretions which are characteristic of the underlying Keuper marls ('Knollen-Mergel'). Third, the sole of the conglomeratic bed is covered by casts of vertical rhizocoralliid spreite burrows, whose perfectly preserved scratch marks suggest that the Keuper marl, into which they were dug, was already well compacted and rather stiff. Such burrows are characteristic of the *Glossifungites* ichnofacies of shallow marine firmgrounds. While other species of the ichnogenus *Glossifungites* are oblique and in the size-class of the related *Rhizocorallium*, the smaller ones at the base of the Jurassic can be compared to the vertical burrows of the modern amphipod *Corophium* and may well be the works of related intertidal crustaceans. In any case these burrows show that the conglomerate is not simply the depositional phase of the event that made the erosion. Rather, the two processes were separated by a quiescent firmground period lasting long enough to allow the establishment of the *Glossifungites* community. Moreover, deposition of the conglomerate bed at this place was not preceded by major erosion, which would have destroyed the burrows.

Nor does the conglomerate bed itself represent a simple sedimentational process. Besides lithoclasts it contains many shells, predominantly of byssate and cemented epifaunal bivalves (*Plagiostoma*, *Lima*, *Entolium*, *Inoceramus*, *Liostrea*). But poorly preserved specimens of *Cardinia* indicate that mud-burrowers were also present originally, but were largely eliminated by diagenetic solution of their aragonitic shells. Accordingly, we interpret this bed as a composite record of muddy periods interrupted by major storm events. These winnowed the mud away, but their erosive effect was stopped by the growing lag of shells and pebbles, which later allowed the colonization by an epifaunal post-event community of epibyssate and cemented bivalves before the mud took over again.

This interplay of sedimentation, shell production and storm reworking, comparable to situations known from modern littoral environments (Seilacher 1985), was periodically interrupted by the deposition of black mud containing the echinoderms, which, unlike the previous and following mud-layers, locally escaped subsequent storm erosion.

The previous style of storm-winnowing, plus the lateral introduction of reworked Keuper nodules, continued in the thicker conglomeratic bed overlying the echinoderm horizon. But its top is modelled by large oscillation ripples, suggesting that the eventual shift to the muddy sedimentation of the Psilonotus Clays happened between the sand and the mud phase of a single tempestite.

(*b*) *Faunal spectrum and preservation*

The well preserved echinoderm fauna (30 asteroid, 15 ophiuroid, 15 crinoid, 40 echinoid specimens; Rosenkranz (1971)) is embedded in the lower 1–2 cm of the clay lens (figure 2, 1–5). It represents an ordinary shelly bottom community with respect to functional adaptation, trophic diversity and age structure. Its only unusual feature is the well articulated preservation in a muddy sediment not corresponding to the substrate on which such forms would normally live. It is surprising, however, that groups other than echinoderms are not equally well represented.

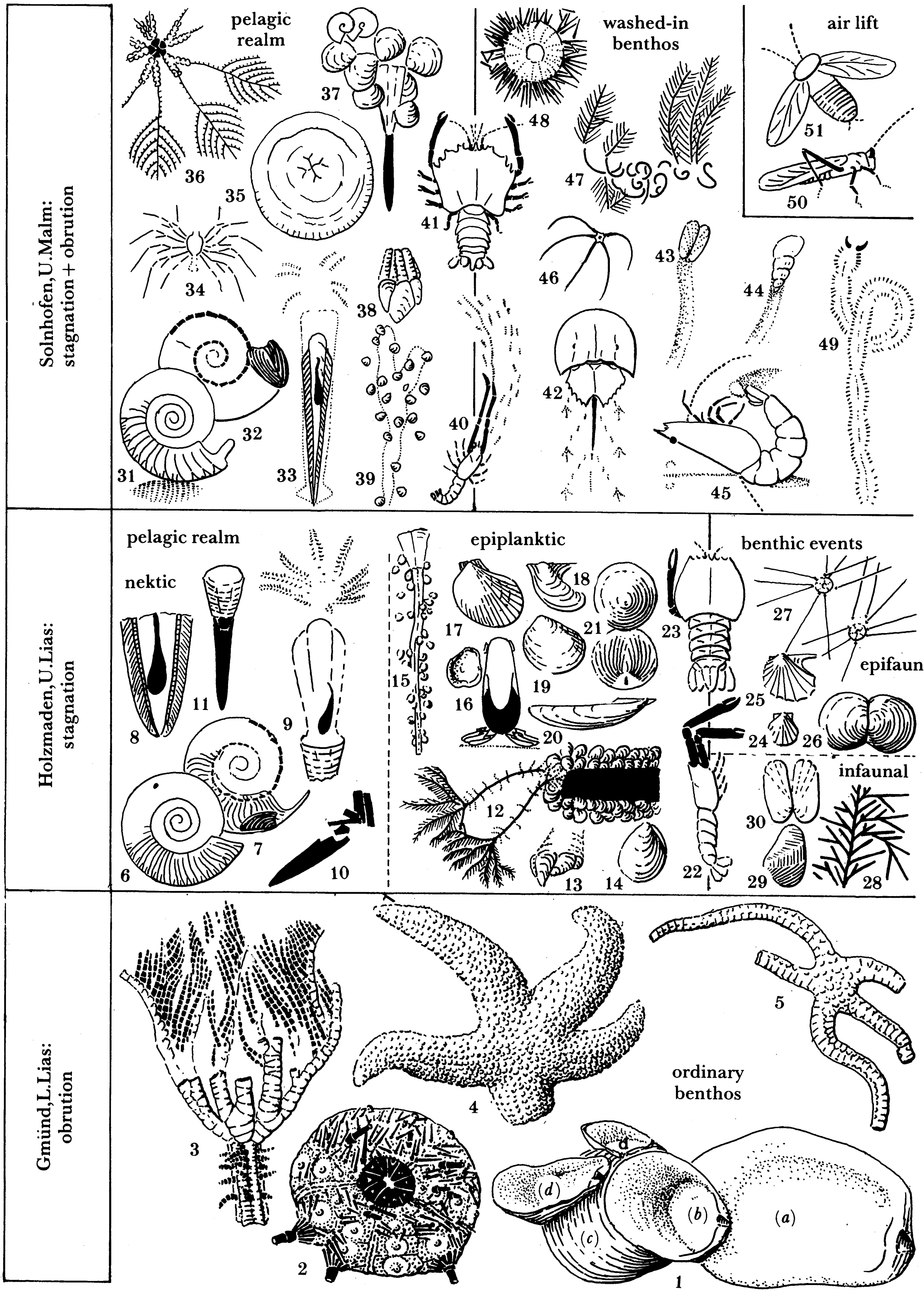

FIGURE 2. For description see opposite.

The only common non-echinoderm associate is a small oyster (*Liostrea irregularis*) which encrusted pebbles as well as shells of its own kind. Such oyster clusters (figure 2, 1) may comprise several generations, the changing orientations of which attest to repeated overturn during an extended exposure at the sediment surface. However, the generations could also represent different shelly phases separated by mud-covered periods. Nevertheless, Rosenkranz found that about 50 % of the oysters on top of the basal shell bed were double-valved and probably became victims of the same event that killed the echinoderms.

In contrast, epibyssal bivalves, being represented within the basal shell bed, are conspicuously lacking on its echinoderm-bearing top.

Rosenkranz's explanation is convincing: the shelly bottom epifauna became buried alive by rapid mud sedimentation. Among the bivalves, this was fatal for the oysters, while pectinids and limids could escape by swimming up. For the echinoderms, however, the fine sediment also had a smothering effect because it blocked their ambulacral systems. It is this 'Achilles heel' that accounts for the high-level taxonomic selectivity of their preservation.

(*c*) *Other examples*

As Rosenkranz (1971) has shown, many, if not the majority of articulated echinoderms in the fossil record are found in a corresponding situation: at the tops of condensed tempestitic

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FIGURE 2. Ecological spectra of representative Jurassic fossil Lagerstätten in southern Germany.

1, Reclining clusters of oysters show sequences of generations separated by overturning (and burial?) events.

2–5, The exclusive, articulated preservation of ecologically diverse echinoderms suggests that they fell victims to a mud-smothering event.

6–11, Among the vertebrates as well as the invertebrates the Holzmaden fauna is dominated by pelagic organisms. Their perfect preservation (associated aptychi, periostracal film and zig-zag siphuncle in ammonites; ink sacks preserved in jet and other soft parts in coleoids 8, 9) suggests rapid settling after death and the absence of benthic scavengers. In the belemnites, only carcasses sunk by predator bites show soft parts (including the non-calcified proostracum, 9), which were otherwise lost during the necroplanktonic drifting stage (11).

12–21, Normally benthic groups are mainly represented by forms attached to floating objects such as drift wood (12–24) and belemnite species whose non-calcified rostrum permitted an extended necroplanktonic drift (15), or to live ammonites (16–21). For details see Seilacher (1982).

22–23, Crustaceans are represented only by very rare specimens of apparently benthic forms. The fact that corresponding species are also found in deposits of the Solnhofen type (40–41; Osteno; Lebanon) suggests, however, that they were not normal benthos.

24–30, Truly benthic organisms (including foraminifers and ostracods) are characterized by small size and monotypic occurrence on particular bedding planes. This suggests that they colonized the mud during benthic events and then became smothered in an articulated fashion. Main representatives are epibyssate bivalve recliners (24–26) and small, long-spined echinoids (27). Endobenthos is represented by tiered *Chondrites* horizons (28) and very rare burrowing bivalves (29, 30 from Riegraf (1977)).

31–36, In Solnhofen the pelagic guild is similar to Holzmaden, but contains additional elements such as crustacean larvae (34), jellyfish (35) and the microcrinoid *Saccocoma* (36, reconstruction), which in places is the most common fossil.

37–39, Epiplankton is less diverse (rarity of ammonites, absence of driftwood may be a reason); but it includes floats assembled by byssate bivalves from necroplanktonic shells of hibolitid belemnites and small ammonites (37). Overgrown seaweeds (39) were probably washed in from the shore.

40–41, Among the diverse crustacean fauna, the common occurrence of *Mecochirus* (40, with trace of death march) and of *Eryon* (41) is reminiscent of Holzmaden.

42–49, In Solnhofen truly benthic organisms do not occur as autochthonous benthic horizons, but as lateral import by turbidity currents. Some of them were still alive enough to leave a short track (42–44), others dead, showing belly-up landing marks (5; figure 5), current orientation (46) or *post mortem* contortion possibly indicative of hypersaline bottom waters. Immobile and burrowing forms (except a rare *Solemya*, 43) were not imported.

50–51, Rare, but extremely diverse insects (most commonly dragonflies), like the flying reptiles and *Archaeopteryx*, represent import by air or surface currents.

shell beds. It could be added that this situation is most likely to occur in the transgressive phases of larger or smaller cycles.

In all cases, smothering by finer sediment is the dominating process, while oxygen deficiency in the pore water (gyttja condition) was either absent or helpful only in the sense that it inhibited infaunal scavengers or bulldozers that would have secondarily disarticulated the buried skeletons.

2. The bituminous Posidonia shales of Holzmaden (L. Toarcian): a stagnation deposit

Since the famous fossil Lagerstätte of Holzmaden and its fossil content have been adequately described (see Kauffman 1981; Riegraf 1984), we can focus here on the points that are important for a comparison with the other examples.

(i) While the Gmünd deposit is at the very base of the Jurassic transgression, the Toarcian marks its peak. This situation favours the establishment of anoxic conditions in many epicontinental basins, whether this is due to changes in the hydrographic regime or to the mobilization of brines from underlying salt deposits (Jordan 1974).

(ii) In contrast to the Gmünd echinoderm bed, here we are dealing with an enormous rock body that spreads over large parts of central Europe with a thickness of tens of metres and representing a time span of the order of millions of years. This difference is important to keep in mind in view of the neverending discussions as to whether we are dealing with a sapropel underneath a stratified, oxygen deficient water body or with a gyttja, in which oxygen deficiency was essentially restricted to the pore water. In such spatial and temporal dimensions, both conditions must be expected at different times and places, as they are in modern stagnant basins (Savrda *et al.* 1984). The question is simply, which situation dominated in space and time and was responsible for the unusual preservation (including soft parts), with which we are concerned here.

(iii) The ambiguity between the two alternative, or rather alternating, models is expressed in contrasting sedimentological as well as ecological evidence. Sedimentologically, the presence of a millimetric lamination that can be correlated over tens of kilometres (H. Roscher, personal communication) as well as landed ammonites that dropped their overgrowth before they eventually tilted over without changing place or position (Seilacher 1982) indicate very quiet water. On the other hand, the orientation and linear accumulation of ammonite shells and other fossils at many levels (Brenner 1976; Seilacher 1982) record uniform currents of up to 20 cm s^{-1}.

(iv) In the ecological spectrum (figure 2, 6–30) we observe the general absence of benthic organisms. Encrusting or reclining brachiopods, bivalves, serpulids and crinoids, otherwise standard elements of Liassic soft bottoms, are represented only as epiplanktonic float on ammonite shells (figure 2, 16–20), belemnite shells with a non-calcified rostrum (figure 2, 15) or drift wood (figure 2, 12–14, Seilacher 1982), while nektonic forms (ammonites, coleoids, fish, ichthyosaurs and plesiosaurs) are the dominant fossils. On the other hand there are individual horizons covered by monotypic small epibenthics, such as diademoid echinoids or byssate bivalves (*Posidonia*, figure 2, 24–26), whose articulated state of preservation would be in conflict with large-scale lateral import. More common are horizons with abundant benthic microfauna (foraminifers, ostracodes; Riegraf 1985), while tiered bioturbation horizons, dominated by the low-oxygen trace fossil *Chondrites* (figure 2, 28; Bromley & Ekdale 1984) are restricted to a few levels, which become more numerous towards the margins of the basin.

This picture is in accord with observations in modern stagnant basins, where benthic faunas decrease in body size and diversity with decreasing oxygen levels and advance towards the centre of the basin during periods of reduced stagnation (Savrda *et al.* 1984). In the shallower Posidonia shale basin, such benthic events were probably brought about by extreme storms, but they allowed only a few generations to flourish before abiotic conditions took over again.

3. The Solnhofen lithographic limestones (Tithonian): an obrutionary stagnation deposit

(*a*) *Stratigraphic and environmental setting*

This fossil Lagerstätte, most famous for the preservation of feathered *Archaeopteryx* and medusae, was formed just before the regressive end of the Jurassic cycle. With a thickness of up to 90 m it exceeds the south German Posidonia Shale, but both its lateral extent (basins a few kilometres in diameter in a buried sponge–reef topography) as well as its time equivalent (0.5 Ma) are considerably smaller. Also different is the scarcity of fossils: had there been no quarries, the unit would have possibly been mapped as 'non-fossiliferous'.

After all the criteria for emergence (*Limulus* tracks interpreted as bird tracks, desiccation cracks, rain drop impressions, etc.) have been discredited, the old lagoonal model is no longer relevant. Most authors now agree that we are dealing with permanently submerged restricted basins, in which storm wave action was confined to a few metres of depth and that there was some kind of stratification in the water body excluding macrobenthos. This stratification had probably the form of a halocline (Keupp 1977) and it is a secondary question, whether or not the resulting stagnation was also expressed by an oxycline. In any case the bitumen content, even if secondarily lost by weathering, was originally lower than in the Posidonia Shales, owing to the higher rate of carbonate mud sedimentation and lower productivity in the surface water.

(*b*) *Ecological spectrum*

As in the Posidonia Shales, the fauna (figure 2, 31–51) is dominated by pelagic organisms. But instead of ammonites, the most common fossil is the minute stemless crinoid *Saccocoma* (figures 2, 36 and 3*b*), whose anatomy and preservation (see below) suggests a medusoid-like mode of life. There is also a large variety of fish and aquatic reptiles, but among these, land-related forms are more common than the open-ocean ichthyosaurs.

Epiplanktonic fauna is also present, but on a broader spectrum of floats. Driftwood is hardly ever found, probably because in such small water bodies it would always be washed ashore. Since ammonites are rarer as a whole, the small percentage of overgrown shells amounts only to a few specimens. Some of them carry oysters, other lepadomorph barnacles (figure 2, 38), which in Holzmaden occur only on wood (figure 2, 13). Instead we find fouled belemnites, not in the form of an encrustation that occurs when the rostra lie at the bottom, but as a loose attachment of byssal bivalves that prefer the conotheca rather than the rostrum (figure 2, 37). Obviously, the now dominant hibolitid belemnites had a longer necroplanktonic drifting time, which made them more attractive for hitchhikers. The common association of several belemnites, or of belemnites and ammonites, in such clusters suggests that the bivalves could actively enlarge their float by byssal assemblage. Algal fronds are yet another kind of float, but in this case we deal with seaweeds that were torn off their rocky littoral habitat by storms and washed into the basin.

Benthic elements are by no means missing in the Solnhofen limestones, but unlike the

Holzmaden situation they never represent autochthonous burrow or other benthic horizons (except perhaps of Foraminifera; Groiss 1967). Instead we are dealing with inhabitants of the shallow margins that became accidentally washed-in. This view is supported by several lines of evidence. Most spectacular are the death marches recorded by tracks behind carcasses in an environment in which other tracks are never found. The length of these tracks relative to the animal is largest in the low-oxygen bivalve *Solemya* (figure 2, 43) and decreases (with decreasing hardiness in *Limulus* (figure 2, 42), *Mecochirus* (figure 2, 40) and *Eryon* (figure 2, 41). Other crustaceans are never found with a track, but the marks left by the dorsal side of *Penaeus* (figure 2, 45 and figure 5, plate 1), or by the dorsal fins of various fish, show that these swimmers were already dead when they landed at the bottom (Mayr 1967).

A second indication is the selectivity of benthic import. With the exception of *Solemya* (figure 2, 43), no endobenthos (including burrows) is represented, neither is sessile epibenthos. Mobile epibenthic species are found, particularly ones that, on perturbation, would be able to swim up, such as *Antedon* (figure 2, 47), *Limulus* (figure 2, 42) and a variety of crustaceans. It is also noteworthy that almost all imported limulids are juveniles not adults, whose much larger sizes can be reconstructed from tracks (not death marches) found in marginal areas of Solnhofen basins (Painten). This could be because juvenile limulids more readily swim up on disturbance and are therefore more prone to be washed away than adults.

(*c*) *Necrolytic features*

A dorsal bend of the vertebral column, comparable to *post mortem* deformations of drying modern carcasses (Schäfer 1955) is a familiar feature in Solnhofen *Archaeopteryx*, *Pterodactylus* and *Compsognathus*, but occurs also in fishes. In the latter case it cannot be a desiccation feature, because associated belly-up landing marks and tail fins disrupted during the bending of the vertebral column (figure 7; Mayr 1967) clearly show that the deformation took place only after the carcass had sunk to the bottom. Therefore it may be assumed that the bottom water was hypersaline to effect the necessary dehydration.

Analogous necrolytic deformations may be observed in articulated skeletons of invertebrates. In a carcass of *Penaeus* (figures 2 and 5) with a belly-up landing mark, the ventral flexure of the tail scraped off sediment after the body had tilted over. A possibly related phenomenon is the contortion of Solnhofen crinoids. In *Saccocoma*, the feather-like form of the arm tips (figure 2, 36) is invariably obscured by intense inward coiling (figure 3*b*). *Antedon*, in contrast, has the proximal parts of the arms intensely coiled (figure 3*c*) and sometimes disrupted (figure 2, 47), while the tips are conspicuously straight. From such deformations we may derive flexibility patterns, and hence the mode of swimming in different species (figure 3*d*, *e*), but we may also take them as environmental signals that seem to be lacking in Holzmaden-type deposits.

(*d*) *Biostratinomic features*

The scarcity of fossils in Solnhofen precludes the statistical measurement of preferred azimuth orientations. Strong currents are indicated, however, by tool and roll marks left by ammonite shells (Seilacher 1963) and other objects. Their association with incipient flute casts further suggests that these currents were sediment-loaded. This is in accord with the preferred position of the Solnhofen fossils at the bases of beds and with the occurrence of grading in other Upper Jurassic occurrences (Nusplingen; Temmler 1964). Turbidity currents are also indicated by

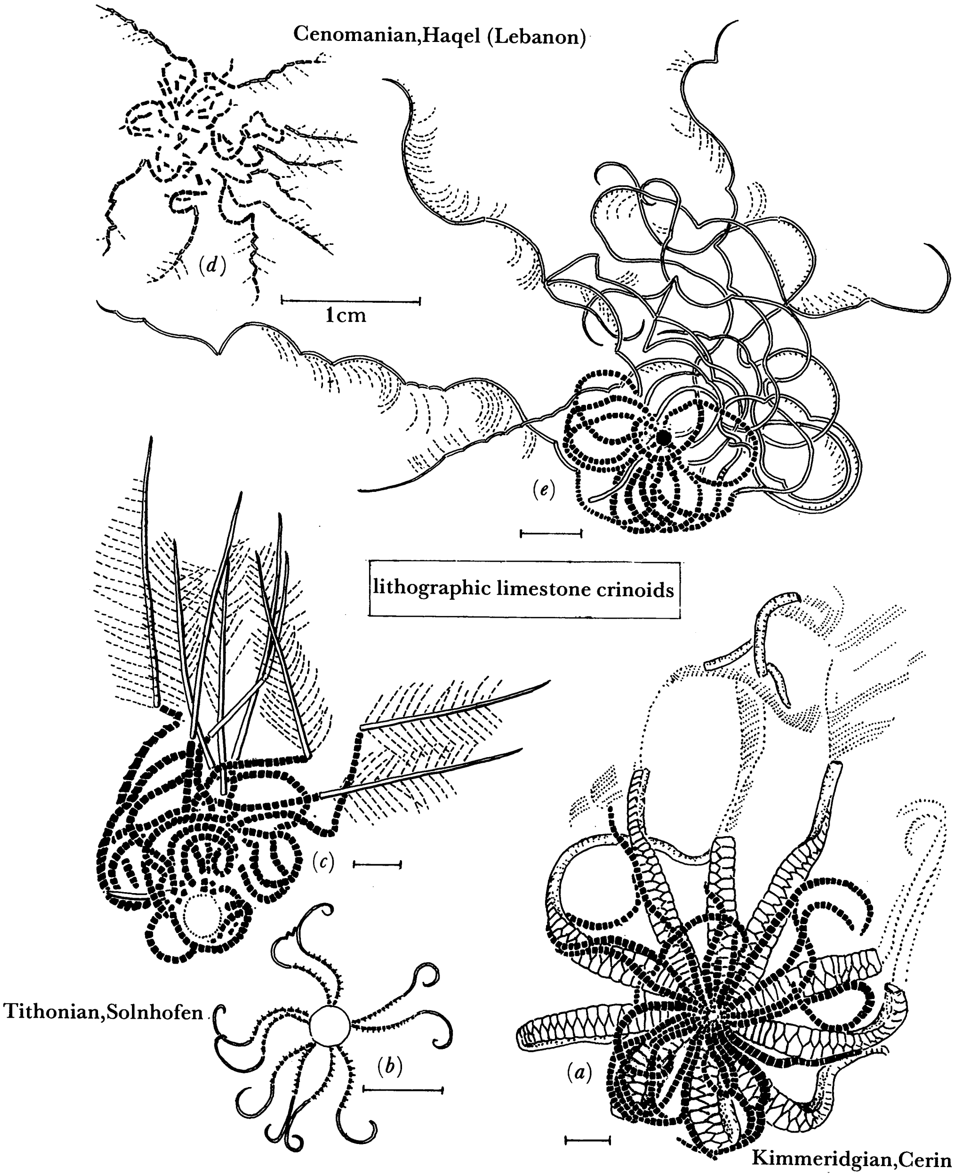

Figure 3. *Post mortem* contortion of echinoderm carcasses in lithographic limestones reveals flexibility patterns along the arms as well as the dehydrating effect of hypersaline bottom waters. (*a*) *Antedon thiollieri*, U. Jurassic, Cerin. Drag marks (dotted) suggest secondary contortion of the arm tips in a current-oriented carcass. (*b*) In Solnhofen *Saccocoma* (GPIT 1630/1) maximum contortion is in the pinnulated arm tips (see figure 2, 36) suggesting that these were the active parts in filter swimming, while the arm bases were held out as an umbrella. (*c*) Solnhofen '*Antedon*', in contrast had stiff arm tips moved as oars by the more flexible proximal parts. (*d*) This small comatulid has a style of contortion similar to (*c*) (GPIT 1630/2). (*e*) In the larger species, proximal arm sections are coiled like in (*c*), while the distal portion deformed in an arcuate fashion (GPIT 1630/3). Scale bars are 1 cm.

the radial current directions mapped from fossil orientations around the much more fossiliferous and better exposed lithographic limestone basins of the Lebanese Cretaceous (Hückel 1970, figure 13), which is in marked contrast to the uniform current directions of the Posidonia Shales (Brenner 1976).

(*e*) *Diagenetic features*

As to be expected in such different lithologies, certain biomaterials suffered different transformations in bituminous shales and lithographic limestones. In Solnhofen, for instance, both vertebrate coprolites and the ink sacks of coleoid cephalopods are phosphatic, while in Holzmaden only coprolites are phosphatized, while the ink is preserved as jet. In both cases, however, mineralization happened so early that these originally soft materials did not become deformed by compaction.

Aragonite solution seems to have been a similarly early process, as shown by the preservational history of ammonites (Seilacher *et al.* 1976). Their compactional deformation, varying with different shell geometries, shows that the aragonite was dissolved not at the surface but within the sediment. On the other hand the plastic lateral deformation of Solnhofen ammonites in slumped layers ('Krumme Lagen') indicates that the shells had already been reduced to periostracal films within a few metres below the sediment surface.

The real problem is not the difference, but the identity of diagenetic signatures in the Holzmaden and Solnhofen cases in spite of their lithological differences. The flattened periostracal foil preservation of empty ammonite phragmocones that the two localities have in common contrasts sharply with 'normal' situations, in which such phragmocones are either lined with pyrite (non-bituminous Liassic black shales; Hudson (1982)) or filled with blocky calcite (micritic limestones of the Upper Jurassic) and are therefore little compacted. This indicates that the special conditions responsible for the exceptional preservation of other fossils were not restricted to the open water, but had an effect also on the pore water system.

(*f*) *Prokaryotic scum: the neglected factor*

Diagenesis is traditionally viewed as the result of physicochemical processes. Within the upper centimetres of the sediment column, however, in which the observed soft-part permineralization and aragonite solution appears to have taken place, chemical conditions are mainly controlled by microbiological activity.

To reconstruct the microbiology of ancient mud bottoms is largely a geochemical task. Still there are a few morphological clues. Scanning electron microscope studies by Keupp (1977) have demonstrated that, apart from coccoliths (Hemleben 1977*b*), coccoid cyanobacteria are

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DESCRIPTION OF PLATE 1

FIGURES 4–9. Cyanobacterial mats, probably a most important factor in preservational processes, can be inferred from indirect evidence. In Solnhofen, their presence is indicated not only by lamination and near-absence of erosion, but also by surface features.

FIGURE 4. Halo of ripped-up scum around swaying fish tail (from Barthel (1978), plate 61, figure 1).

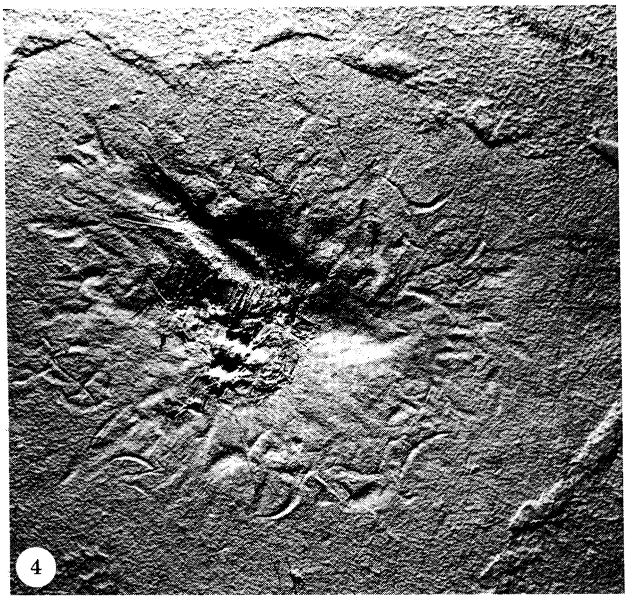
FIGURE 5. Preservation of landing marks (rostral carina, eye tips, abdomen) besides a fallen-over carcass of *Penaeus* and of scrape mark plus scum heap produced during *post mortem* inflection of tail end (GPIT 1630/4).

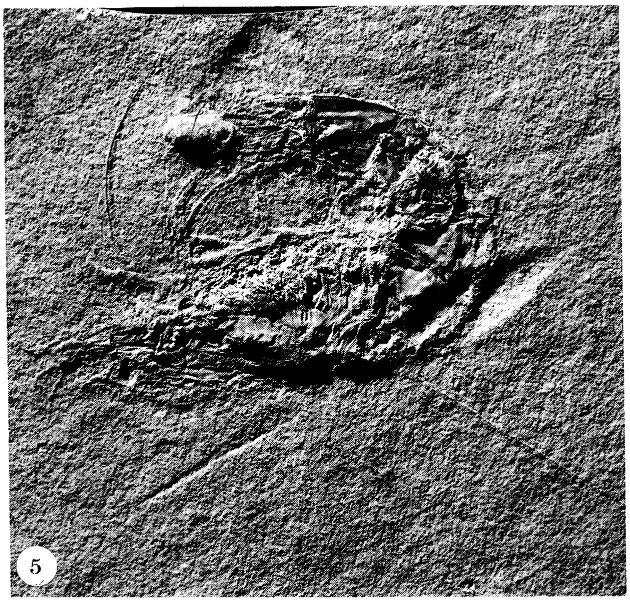
FIGURE 6. Ruffling around roll mark of an ammonite shell (GPIT 1630/5) and drag marks (Eichstätt Museum).

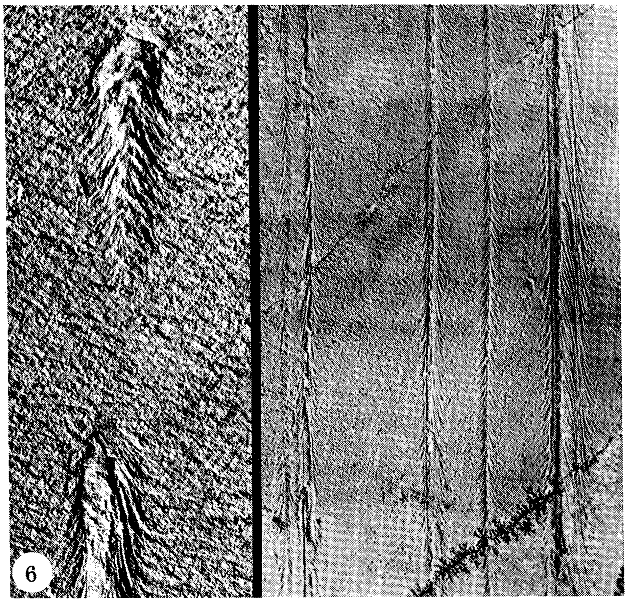
FIGURE 7. Cast of reticulate ridge pattern (bottom surface, GPIT 1630/6) around fish with *post mortem* contortion of vertebral column.

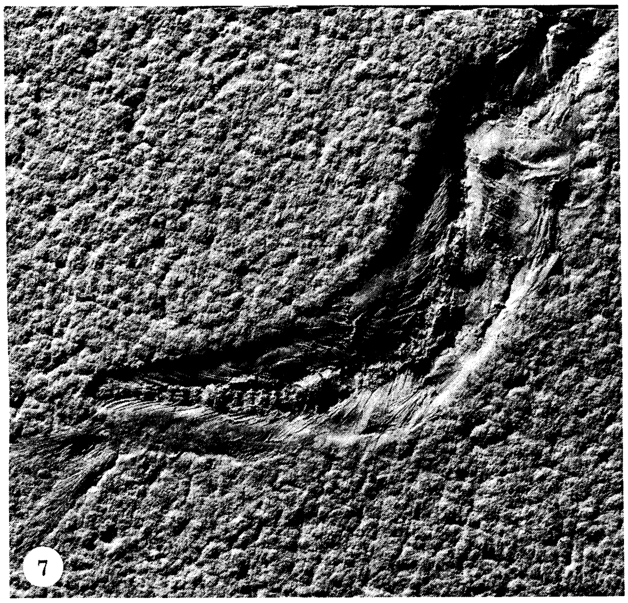
FIGURE 8. Radial arrangement of such ridges around an ammonite shell, whose 'pedestal' elevation is a later diagenetic feature. (From Janicke (1969), plate 6, figure 4.)

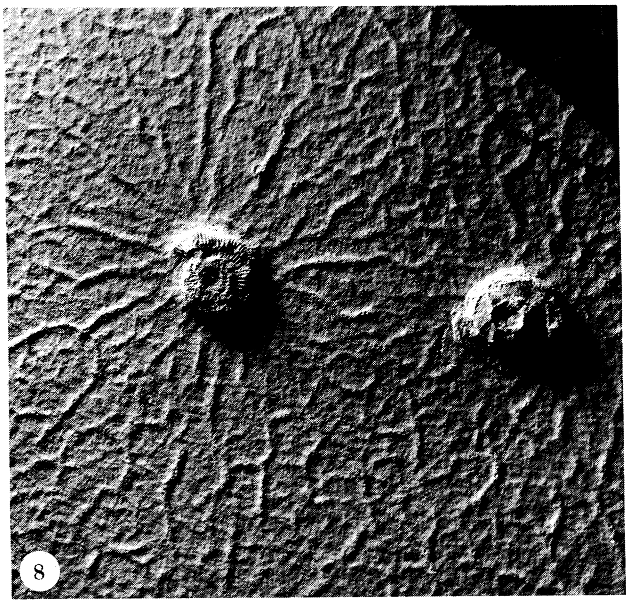
FIGURE 9. Corresponding pattern produced by mechanical creasing of a depressurized blister. (Courtesy of Professor Frei Otto, University of Stuttgart.)

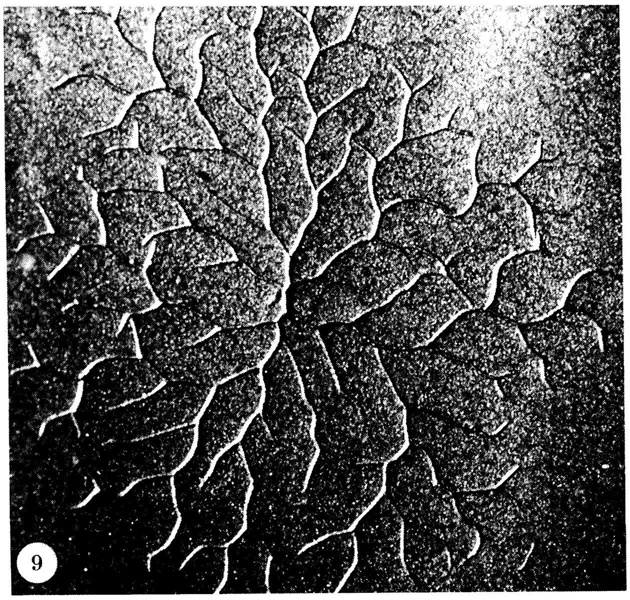












FIGURES 4–9. For description see opposite.

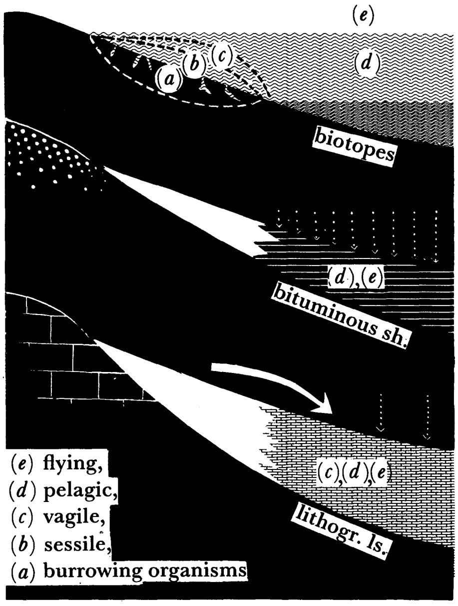


FIGURE 10. Stagnant basins of the Holzmaden type (mostly bituminous shale facies) and Solnhofen type (lithographic carbonates) both lack autochthonous benthos (except during short benthic events) and are dominated by drop fauna. The geometry of Solnhofen-type basins, however, allows also the lateral import, by turbidity currents, of littoral benthos, preferably of vagile forms.

a major constituent of the Solnhofen muds. Their presence is also expressed macroscopically by a scum on the bed surface. This scum allowed tracks and roll marks to be preserved, caused the ruffling of roll and drag marks (figure 6; Mayr 1967, plate 13, figures 1–3) and was visibly ripped off around a swaying fish body (figure 4). Its presence is also expressed by reticulate ridges on the tops of Solnhofen beds (figure 7), which have been variously explained as rain drop impressions (Mayr 1967), syneresis cracks (Janicke 1969) or load casting. Their radial arrangement around an ammonite (figure 8), however, suggests that we deal with the creasing of a film similar to the tepee structures of modern algal mats or the mechanical creasing of blister membranes (figure 9). From other evidence Hemleben & Freels (1977*a*) have considered such prokaryotic scum as the chief factor in the Cretaceous lithographic limestones of Hvar, Yugoslavia.

Today, cyanobacterial films of this kind are largely restricted to hypersaline environments. But, like cyanobacterial stromatolites, they could have had a much wider distribution in earlier times, particularly in the Precambrian. Their effect would be (Keupp 1977): (i) to protect soft sediments against erosion; (ii) to favour the preservation of tracks and other markings; (iii) to serve as food source during benthic events; (iv) to protect carcasses against decay; (v) to act as a 'carbonate pump' into the sediment (Walker & Diehl, this symposium); (vi) to seal the particular microenvironment responsible for the absence of bioturbation (Krumbein 1983) and for the unusual preservational histories of ordinary fossils such as ammonite shells.

As yet, this eludes macroscopic investigation, but it may become more transparent through ultramicroscopic studies in ancient rocks and particularly through microbiological and geochemical analyses in adequate modern environments.

4. Other examples

As epitomized by the faunal spectra and modes of preservation, the Holzmaden and the Solnhofen deposits have obviously much in common. Differences are minor and largely explained by the different palaeogeographic frames (figure 11). On the one hand we have a large stagnant basin with little influx from the margins, but with the possibility of storm-induced water-mixing and the short-term establishment of small-sized and monotypic benthic faunas. In the much smaller basins of the Solnhofen type, storms could affect only the shallow margins; but the steeper slopes favoured the episodic introduction, by slumping and turbidity currents, of fine-grained sediment and transportable benthic organisms from the more oxygenated nearshore environments. In such an event, the imported bodies (some still alive) would reach the bottom first, soon to be covered by the mud settling from suspension. Therefore, we would define the Solnhofen lithographic limestones primarily as a stagnation deposit, but one in which obrution was also an important factor.

There are many counterparts to these two types in the Phanerozoic record, each with minor but significant pecularities. Thus the bituminous shales of the Lower Lias of southern Germany (Ölschiefer, Sinemurian) resemble Holzmaden except that, due to the thickness of only a few decimetres and poor outcrops, their fauna is much less spectacular; but they do contain benthic horizons of small echinoids (‘*Cidaris*’ *olifex*) as well as tiered bioturbation horizons. Equally comparable are the Upper Triassic bituminous shales of southern Switzerland, but the shales themselves lack periostracal impressions of ammonite shells, which are only found in the hard dolomitic layers, where they were fixed by early diagenetic cementation (Rieber 1973).

A less stagnant modification of the Holzmaden type is found in marginal areas of the Toarcian basin, where benthic horizons are more common and the aragonitic ammonite shells are not dissolved. The same appears to be true for parts of the Oxford and Kimmeridge clays in Britain, where the benthic element includes reclining and bone-encrusting oysters (Martill, this symposium; Aigner 1980). Nevertheless, the shales are bituminous and vertebrate skeletons have remained articulated.

The sponge reef topography and the regression of the Upper Jurassic has led to the formation of lithographic limestones in other parts of central Europe also. In Nusplingen (south of Tübingen) fauna and preservations are similar to Solnhofen except that *Saccocoma* is lacking, some beds are clearly graded and the mud consists largely of sponge spicules, indicating that sponge reefs around the small basin were still growing (Temmler 1964, 1966). The faunal difference of the French locality of Cerin may be largely due to its slightly older age (Kimmeridgian, Bernier *et al.* 1983). In this case, however, the muds did at times emerge, as shown by horizons with dinosaur tracks.

The most similar extra-Jurassic representatives of the Solnhofen type are in the Cretaceous of Lebanon. These lithographic limestones are associated and interbedded with huge slump masses in what appear to be rhythmically subsiding pull-apart basins related to the nearby Jordan rift system (Hückel 1970; Hemleben 1977*a*). Fossils are very common and diversified, with washed-in benthos dominating over the pelagic rain. *Post mortem* contortions of fish and echinoderm skeletons (figure 3) suggest a halocline. In the mid-Triassic lithographic rocks of Alcover (Spain; Esteban Cerda *et al.* 1977; Via Boada 1977; Hemleben & Freels 1977*b*) the relation to an ancient reef topography in a regressing sea resembles Solnhofen. Minor differences in preservation are due to the dolomitic nature of the rock, which, together with gypsum crystals, also suggests increased salinity in this case.

Identification becomes more difficult with increasing temporal distance from the Jurassic-type examples. The lithographic limestones of Monte Bolca (Eocene, N Italy; Sorbini 1983), probably deposited in a volcanogenic topography by graded turbidite sedimentation, can still be compared to Solnhofen, although many index groups of organisms have fallen victims to the Cretaceous extinction. But what about the 'lithographic' Green River Shales (Eocene) of North America? Being deposited in a basin too large to produce turbidity currents, are they rather a stagnation deposit comparable to the Posidonia shales, but in a salinity régime that favoured bacteria-mediated carbonate precipitation? Similarly enigmatic is the case of the thin-bedded chalks of the Niobrara formation. In addition to the famed vertebrate skeletons and the floating crinoid *Uintacrinus* they contain *Inoceramus* shells that appear too large to have been epiplanktonic. However, the double-valved, closed preservation of these giant bivalves, equal encrustation on both valves and their lying always on the same valve does not either fit a reclining mode of life. Also reclining oysters, which are such a regular element in other chalks, are conspicuously absent. Could it be that the Niobrara chalks are the equivalent of a dark bituminous shale at a time when excessive planktonic carbonate production diluted the sapropel into a white mud without the necessity of lateral carbonate import?

On the other hand, the Lower Liassic deposits of Osteno (see Pinna, this symposium) are dark-coloured, finely laminated and bituminous. But they consist, like the lithographic limestones of Nusplingen, largely of sponge spicules. Also their faunal spectrum relates them to Solnhofen rather than to Holzmaden, with crustaceans, worms and other washed-in benthos dominating over the pelagic guild and with benthic events (including bioturbation horizons) being completely absent. The preservation of the rare ammonites also resembles Solnhofen (flattened, non-pyritized, zig-zag siphuncle).

What we can learn from the comparisons so far is that lithology, colour and bitumen content should not be taken as the primary criteria in a genetic classification of fossil Lagerstätten, because they may change with the hydrographic situation and with shifts in biological carbonate mud production. Nor should the salinity factor be rated too highly.

The Jurassic deposits of the Karatau (Kazakhstan), for example, are a valid counterpart of the Solnhofen situation although they were deposited as dolomitic muds in a tectonic, probably hypersaline lake, in which the 'washed-in benthos' is mainly replaced by river-imported insects.

Also deposited in a tectonic lake are the Eocene shales of Messel, Germany (Franzen, this symposium). Their ecological spectrum (fishes, washed-in land and flying vertebrates, insects) resembles Karatau, but this sediment is bituminous and non-calcareous without indications of increased salinity. Nevertheless the complete absence of autochthonous benthos suggests that the stagnant condition was permanent and not interrupted by either storms (small basin geometry) or floods (thermocline).

Environmental identifications become still more difficult if we deal with Palaeozoic or even Precambrian examples because modes of life are increasingly difficult to assess. There is no problem in tracing back the obrution deposits of the Gmünd type as long as we have echinoderms to go by. The Holzmaden type is also well represented by bituminous shales such as the Ohio shales of the Upper Devonian and Lower Carboniferous of the eastern United States (Barrow & Ettenson 1980). But we do have problems to identify the Solnhofen type.

The Silurian Mississinewa shales of Indiana, for instance, were deposited in inter-reef basins, in which a turbiditic mode of sedimentation is indicated by grading and position of the fossils at the bases of the silty dolomite beds (Erdtmann & Prezbindowski 1974). But the fauna is more diverse than in Solnhofen and includes such immobile benthic forms as sponges, brachiopods and a large variety of dendroid graptolites. Also the beds are commonly bioturbated from the top, indicating a rather diversified autochthonous benthos. But the dominant dendroid graptolite genus is *Dictyonema*, generally taken to have been pelagic. Also there are many kinds of cephalopods (little compacted, but not pyritized) and perfectly, three-dimensionally preserved crinoid crowns, whose arms and pinnules are integrated into an umbrella that would fit a pelagic mode of life well. Thus we are dealing with a similar situation to Solnhofen combined with a benthic element unfamiliar in Mesozoic lithographic limestones. There appears to be some similarity, however, to argillaceous dolomites of similar age in Wisconsin (Mikulic *et al.*, this symposium).

Also unfamiliar, from a Mesozoic point of view, are the Hunsrück Shales of the Lower Devonian of Germany (Kuhn 1961; Seilacher & Hemleben 1966), because they combine soft-part preservation (non-mineralized skeletons of arthropods; articulation) with pyritization and a diverse benthic fauna including a variety of burrows. Silty microturbidites are a common element that also allows the preservation of various arthropod tracks. Current action is also indicated by sedimentary structures and fossil orientations, while wave ripples are conspicuously absent. These features and the predominance of echinoderms suggest that obrution was the major factor; but oxygen deficiency must also have been involved, if only in the form of gyttja, to allow soft-part preservation. It is also noteworthy that the echinoderms lack *post mortem* contortions.

Still stranger forms of conservation deposits are represented in the Cambrian. Among these we note the combination of a trilobite shell hash suggestive of storm winnowing with a bituminous lithology and phosphatized arthropod 'soft parts' in the Upper Cambrian Alum Shales (Müller; this symposium) and, of course, the famous Burgess Shale (Collins *et al.* 1983; Conway Morris, this symposium). Here the problematic nature of many fossils and the absence of more familiar groups such as echinoderms and molluscs make it difficult to interpret the ecological spectrum. As a whole, the benthic element appears to dominate in the Burgess Shale, but in a washed-in rather than a benthic-event fashion. However, there are some assumed pelagics such as *Marrella*, the most common faunal element. This looks like the Solnhofen spectrum, though a non-carbonate version. The discovery of new localities in addition to the classical one suggests, however, that we deal not simply with a unique physical setting, but that a kind of time signature is also involved.

The most challenging problem in this respect is the classification of the Ediacara-type conservation deposits of Vendian age (Fedonkin, this symposium): a task that is largely independent of the taxonomic problems involved (see Seilacher (1984) and this symposium). There is no question of dealing with the impressions of soft-bodied organisms in a sandy facies that contrasts with the fine-grained sediments discussed so far.

It is true that we do know sandy obrution deposits also in the Phanerozoic. But they refer to vertebrate skeletons in continental régimes, to exceptional turbidite events (fish deposit of Sendenhorst; Siegfried 1954) or to sand-smothered echinoderms (Seilacher 1968) and not to soft-bodied organisms. The Vendian fossiliferous sandstones, in contrast, appear to be largely storm-generated (Goldring & Curnow 1967), that is, depositionally similar to many shallow marine sandstones in the Phanerozoic, in which such soft-body impressions never occur. To invoke for this unusual preservation a unique physiographic constellation is no more justified, given that Ediacara-type fossils have been found in more than 20 localities all over the world (Glaessner 1984, figure 1.8) and also in sandstones that are claimed to be deep-water turbidites

(Anderson & Conway Morris 1982). Clearly this preservation must be due to an 'anactualistic' factor (in a Phanerozoic view) of a more global nature.

It has been claimed that this factor was a lack of bioturbation. But burrows made by worm-like organisms and possibly coelenterates have been found in many Ediacaran fossil localities and with surprisingly advanced sediment feeding strategies. It should also be remembered that microbial degradation would destroy a shallowly buried soft-bodied carcass. A more relevant clue may come from sedimentological data (J. Gehling, unpublished, and personal observations in the field). They suggest the presence of a rather resistant cyanobacterial scum that protected these sand surfaces against storm erosion and amalgamation and allowed flexible sand-shards to be ripped off. This would go along with the general impression that cyanobacterial mats (with or without stromatolitic structures) were much more widespread in Precambrian than in later environments; but in exactly what way this non-uniformitarian feature should have influenced the preservation of soft-bodied organisms still remains to be explained.

5. CONCEPTUAL FRAME AND CLASSIFICATION

Our short review of conservation deposits is admittedly very incomplete. For instance it does not cover a group that we previously called 'conservation traps' (Seilacher & Westphal 1971), which is a holding bag for such different cases as mammoths in permafrost crevices, amber insects or bogs. Of significance in our present discussion are only the early diagenetic concretions in the form of coal balls (Scott & Rex, this symposium), 'orsten' (Müller, this symposium), Mazon Creek nodules (Baird *et al.*, this symposium) or the Lower Cretaceous fish concretions from Brazil (Müller, this symposium). Certainly, such concretions are important in that they facilitate fossil hunting and that they provide, through the right preparation techniques, relatively uncompacted fossils. But in a genetic sense, they are only a subset of stagnation (and obrution?) deposits.

In the Posidonia Shales, for instance, beautifully preserved reptiles, fish and coleoid cephalopods come from such concretions; but most of the nodules are barren and most of the fossils are found in layers in which no such concretions occur.

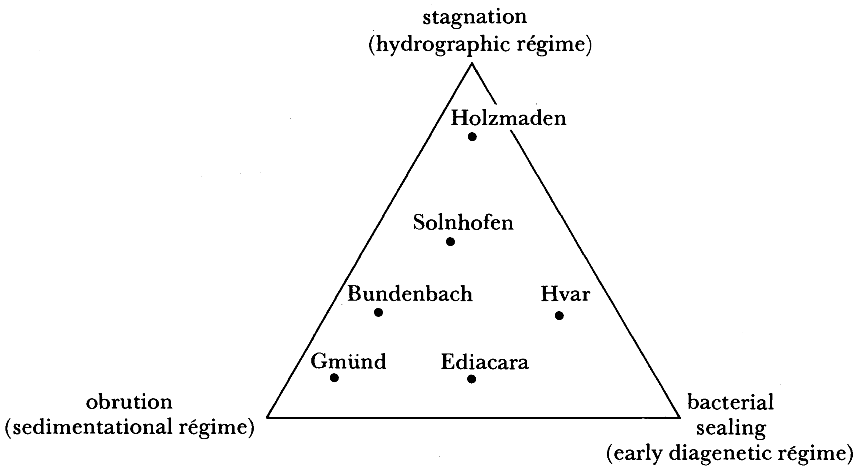


FIGURE 11. Among the many factors involved in the formation of conservation deposits, stagnation, obrution and cyanobacterial sealing are considered the most dominant. They define a conceptual continuum, into which particular examples may be 'mapped'.

TABLE 1. TENTATIVE QUESTIONNAIRE FOR CONSERVATION DEPOSITS

Tübingen questionnaire
Fossillagerstätten
Conservation deposits

- (1) basin situation
  - size (km): 10^{-1} 10^{0} 10^{1} 10^{2} 10^{3}
  - setting:
    - oceanic
    - epicontinental
    - terrestrial
  - origin:
    - tectonic
    - volcanic
    - astroblemic
    - subrosional
    - recifal
    - sedimentary
    - glacial
  - geographic frame:
    - limestones
    - clastics
    - crystalline
- (2) stratigraphy
  - thickness (m): 0.01 0.1 1 10 100
  - duration in absolute time:
  - vertical context:
    - transgressive
    - peak transgression
    - regressive
    - fining-up cycles
    - coarsening-up cycles
  - lateral sequence:
- (3) sedimentology
  - lithology:
  - biograins (coccoliths, forams, radiolarians, spicules, etc.):
  - sedimentary structures:
    - lamination (varves, algal, etc.)
    - slump horizons
    - graded horizons
    - current ripples
    - wave ripples
    - emersion marks (tidal channels, mud cracks, etc.)
- (4) geochemistry
  - evaporitic precipitates (aragonite, calcite, dolomite, gypsum, halite):
  - pyrite concretions (globular, discoid):
  - isotopic deviations:
  - C_{org} (particles, kerogene, bitumen):
- (5) taxonomic spectrum
  - dominated by (priority):
    - echinoderms
    - cephalopods
    - vertebrates
    - crustaceans
    - trilobites
    - others:

locality:
age:

- (6) ecological spectrum
  - burrows (episodic, continuous):
  - tracks (with or without bodies):
  - endobenthos:
    - hemisessile
    - vagile
  - epibenthos (episodic, continuous):
    - sessile
    - vagile
    - able to swim
  - pelagics:
    - nekton
    - floaters
    - epiplankton (on wood, cephalopod shells, live or dead)
  - terrestrial organisms:
    - tracks
    - skeletons
    - land plants (twigs, leaves, trunks)
    - flyers
- (7) necrolytic criteria
  - death marches:
  - landing marks (live, dead):
  - soft parts (impressions, films):
  - organic cuticles:
  - articulation (vertebrates, echinoderms, arthropods, bivalves, aptychi):
- (8) stratinomic criteria
  - life positions:
  - roll marks (of what?):
  - convex up or down:
  - current orientation (azimuth):
  - wave orientation (azimuth):
- (9) diagenetic criteria
  - aragonite preservation (what?):
  - early aragonite solution (composite casts):
  - pyritic steinkerns:
  - concretionary cementation (nucleus, pressure shadow, buckle, pedestal):
  - compactional deformation
  - incoalation:
  - phosphatization (of what?):
  - replacement (shells, bones):

General conclusions:
- stagnation (thermal or halocline):
- obrution:
- algal sealing:

In spite of its incompleteness this review has shown, however, that, apart from the two principal factors of stagnation and obrution and their various combinations, a large number of palaeogeographic, biological, sedimentological, diagenetic and time factors may contribute to the formation of conservation deposits. The result is that each case has a 'personality' that defies rigorous classification.

Of course, there is some virtue in typological groupings. Thus we may distinguish between marine, hypersaline, lacustrine and swamp deposits, or between vertebrate, echinoderm, arthropod and plant Lagerstätten. Or group into Solnhofen, Holzmaden, Bundenbach and Burgess types of deposits. Grouping according to age (Conway Morris, this symposium; Walker & Diehl, this symposium) may also be revealing. But while being useful to emphasize patterns, such classifications can never be binding, because unlike in taxonomy there will be no agreement as to which criteria should have primacy.

Nevertheless we should not be content with descriptive registrations. Instead of expecting the classification to provide a standard set of pigeon holes, we should better consider it as a conceptual framework for heuristic purposes. In figure 11 we propose to use the critical hydrographic, sedimentational and early diagenetic exponents to define a triangular space into which each particular case can be mapped. In addition, we present a tentative questionnaire (table 1) in order to standardize this mapping job, in which by necessity a large number of specialists must be involved.

What lies in front of us, is more than fossil hunting, the unravelling of taxonomic relationships and facies analysis. Expanded over the whole fossil record, a comparative analysis of fossil Lagerstätten could become a genuine contribution of palaeontologists to the integrated view of Earth history.

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Discussion

R. Riding (*Department of Geology, University College, Cardiff CF1 1XL, U.K.*). I wish to query use of the term obrution. Reference to stagnation and smothering (obrution) as alternative modes of formation of conservation Lagerstätten is slightly confusing because stagnation indicates the nature of the environment whereas smothering is a type of asphyxiation. It would be clearer in this case to refer to rapid burial rather than to smothering. Stagnation and rapid burial could then be regarded as different processes, either of which can result in the asphyxiation of organisms. Asphyxiation occurs above the substrate in the case of stagnation and below it in the case of smothering. This usage then clearly distinguishes environmental conditions (stagnation, rapid burial) from the actual mode of death which is, in both cases, asphyxiation.

E. N. K. Clarkson (*Grant Institute of Geology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, U.K.*). The Lower Lias obrution deposit at Gmünd is, as Dr Seilacher has noted, dominated by echinoderms and he had suggested that in such a case the active elements in the benthos might have escaped, whereas the echinoderms could not.

Is it possible to distinguish such an obrution deposit from one in which the original fauna was dominated by echinoderms and little else? I ask this with particular reference to some horizons rich in intact echinoderms in the Scottish Silurian.

H. B. Whittington, F.R.S. (*Department of Earth Sciences, Sedgwick Museum, University of Cambridge*). The Burgess Shale fauna includes the hard parts of characteristic Middle Cambrian animals – trilobites, sponges, brachiopods, molluscs, hyolithids and echinoderms – as well as a remarkable soft-bodied fauna. I have argued in detail (Whittington 1971) that *Marrella* was a benthic animal, the thousands of specimens having been buried in varied orientations in the deposit resulting from a turbidity current. The highly fossiliferous layers in the Phyllopod bed of the Burgess Shale appear to originate from such a mode of transport and burial (Whittington 1980). Comparison with the Solnhofen deposit would thus involve consideration of a similar mechanism for its formation.

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A. Seilacher. 'Obrution' means rapid burial, whether this process only preserved carcasses or also killed the organisms. But only in the latter case can we expect a selective preservation. In the meantime, the analysis of clustered trilobites that appear to have been selectively killed and then buried by the muddy clouds of storm events has added another beautiful example of such obrution deposits. Whether the striking absence or under-representation of non-trilobites or non-echinoderms in these cases be considered an original feature or the outcome of better resistivity to such accidents is a matter of ecological taste.

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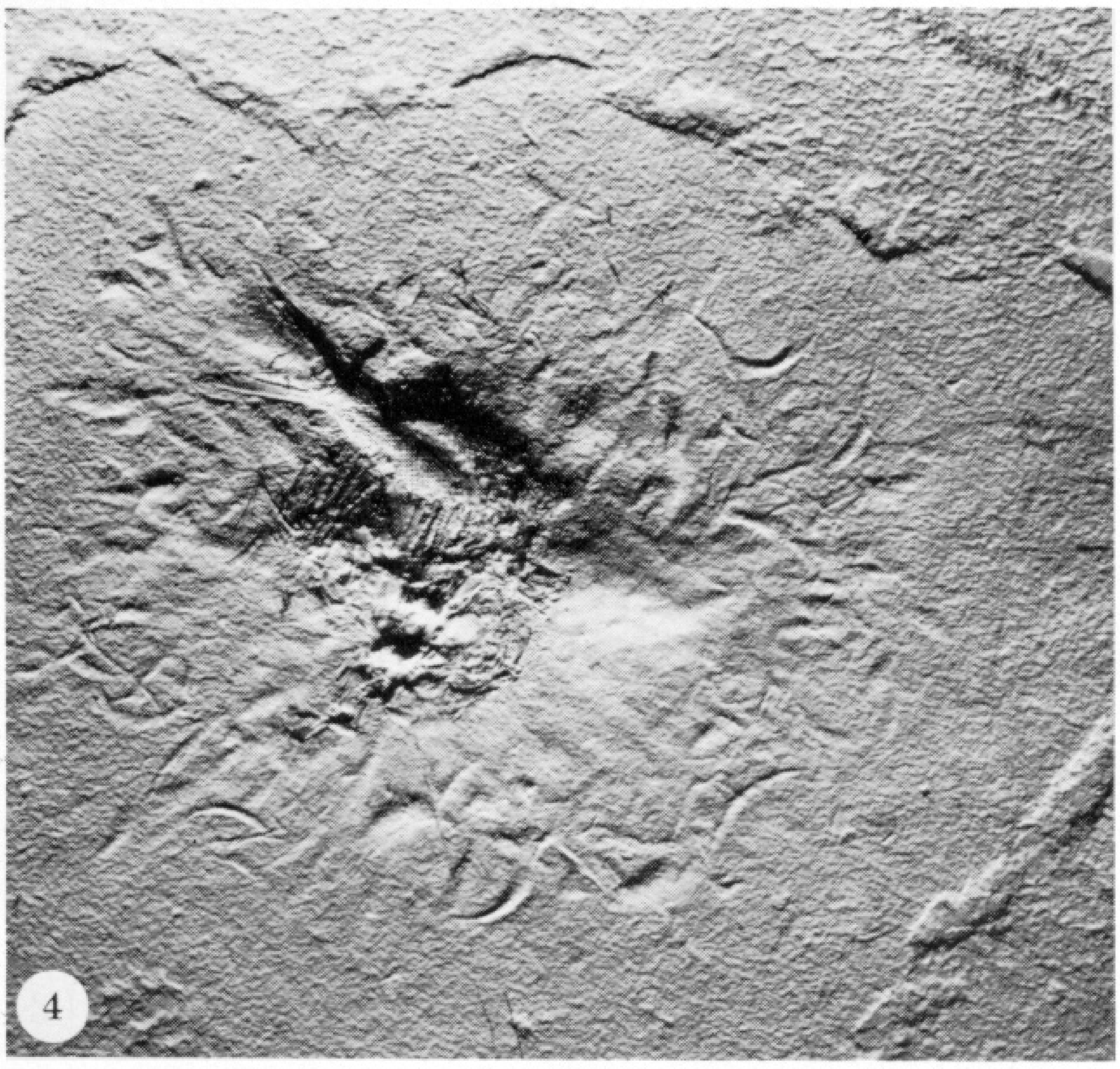
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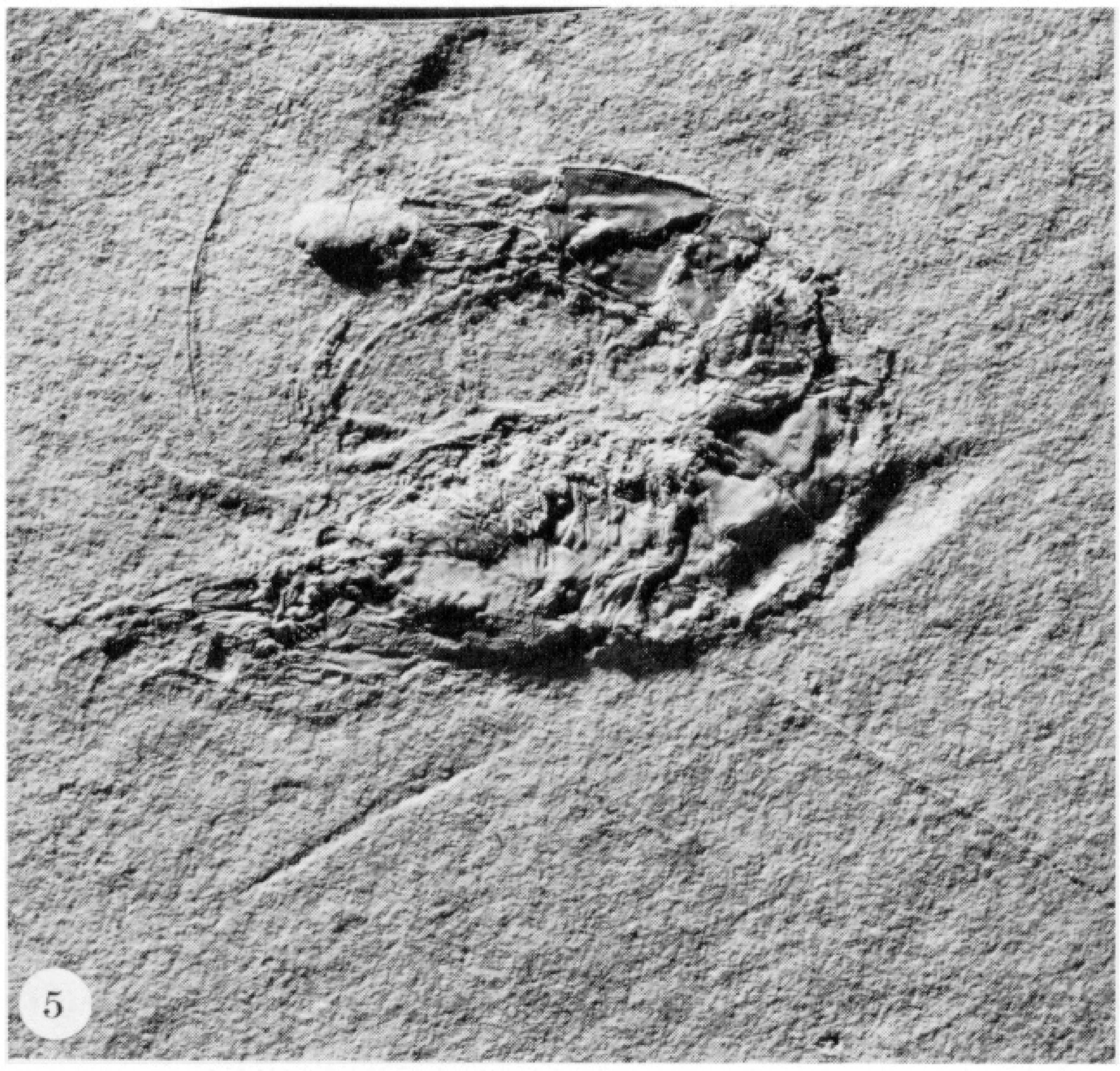
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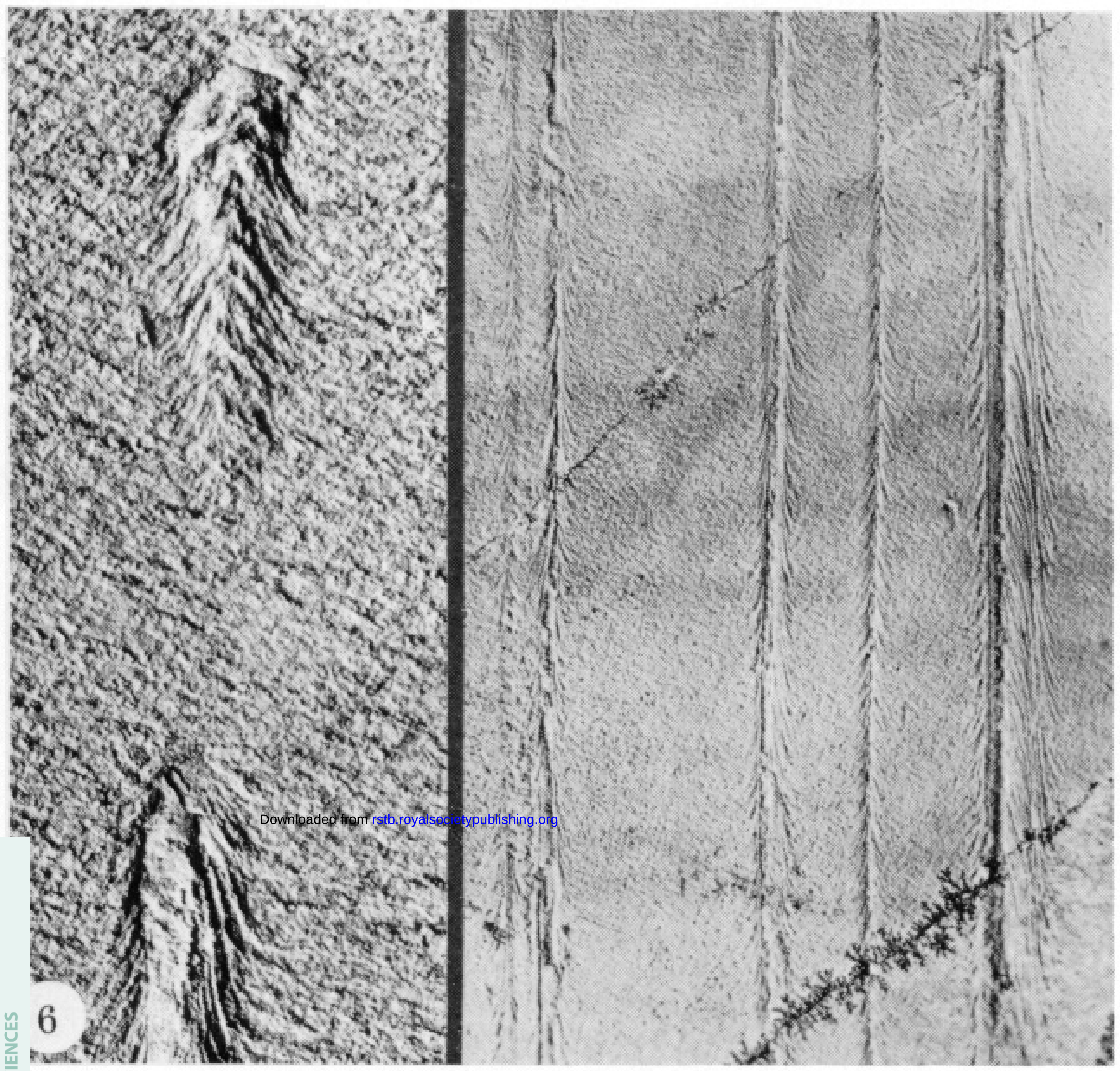
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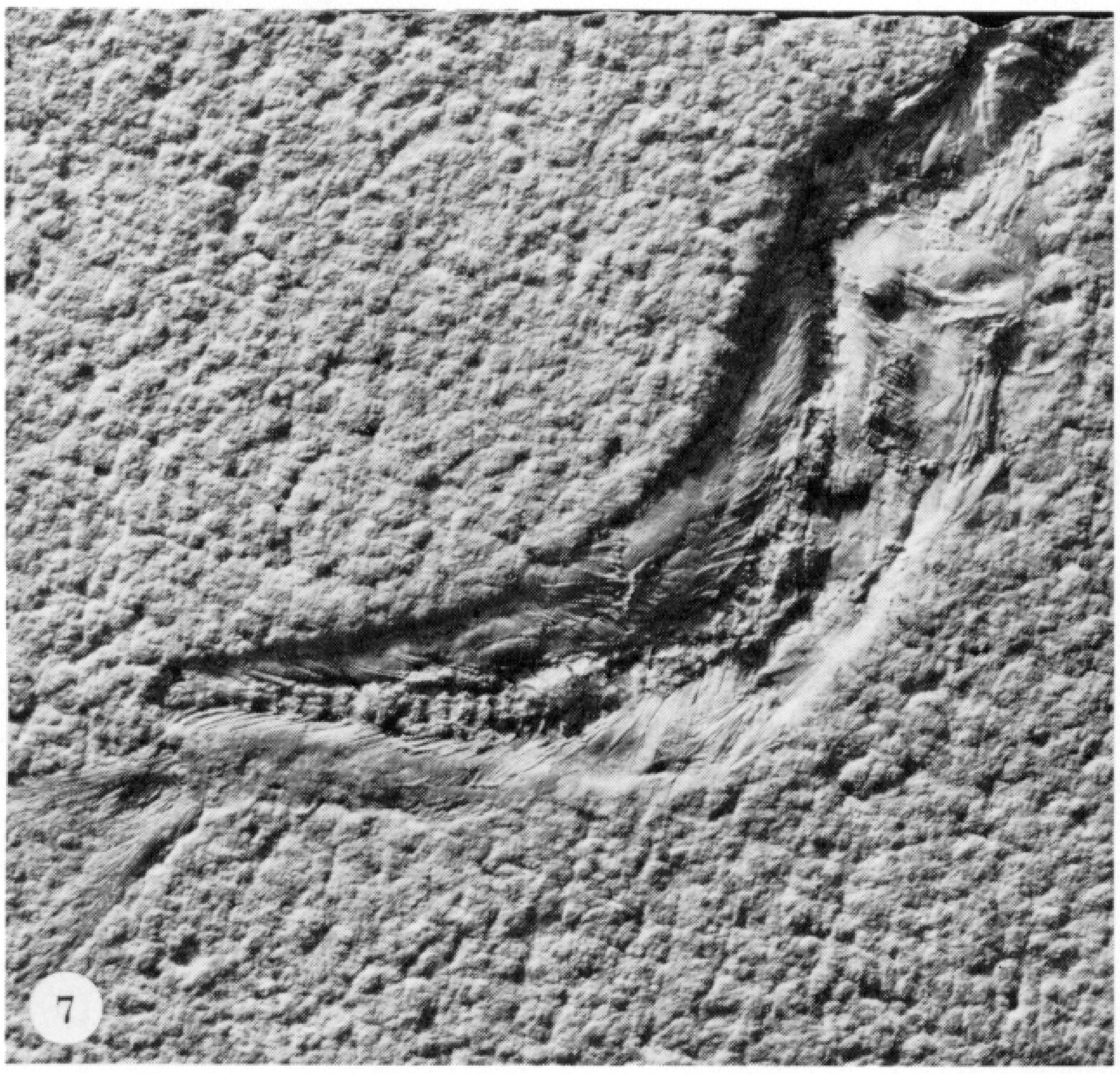
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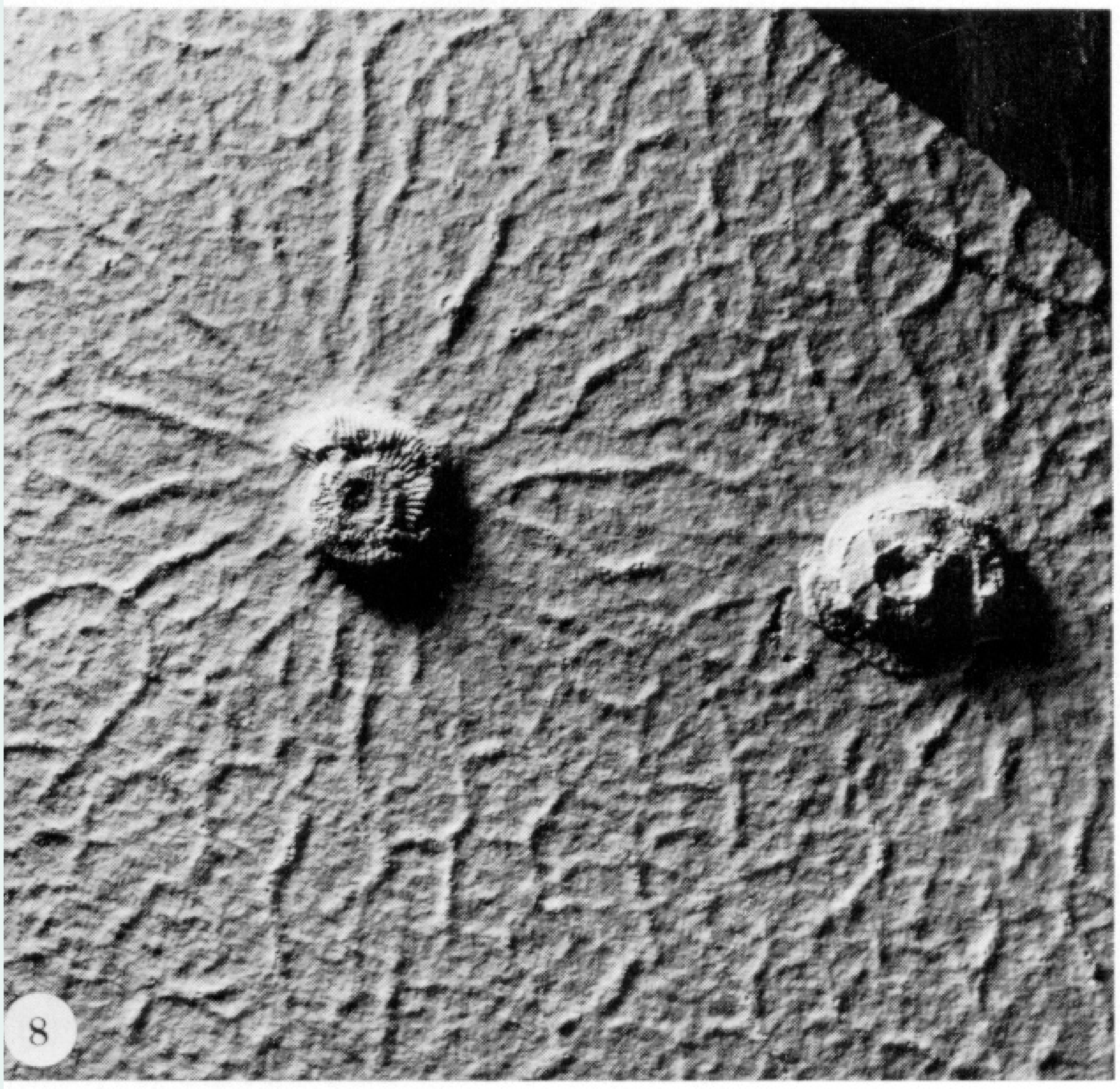
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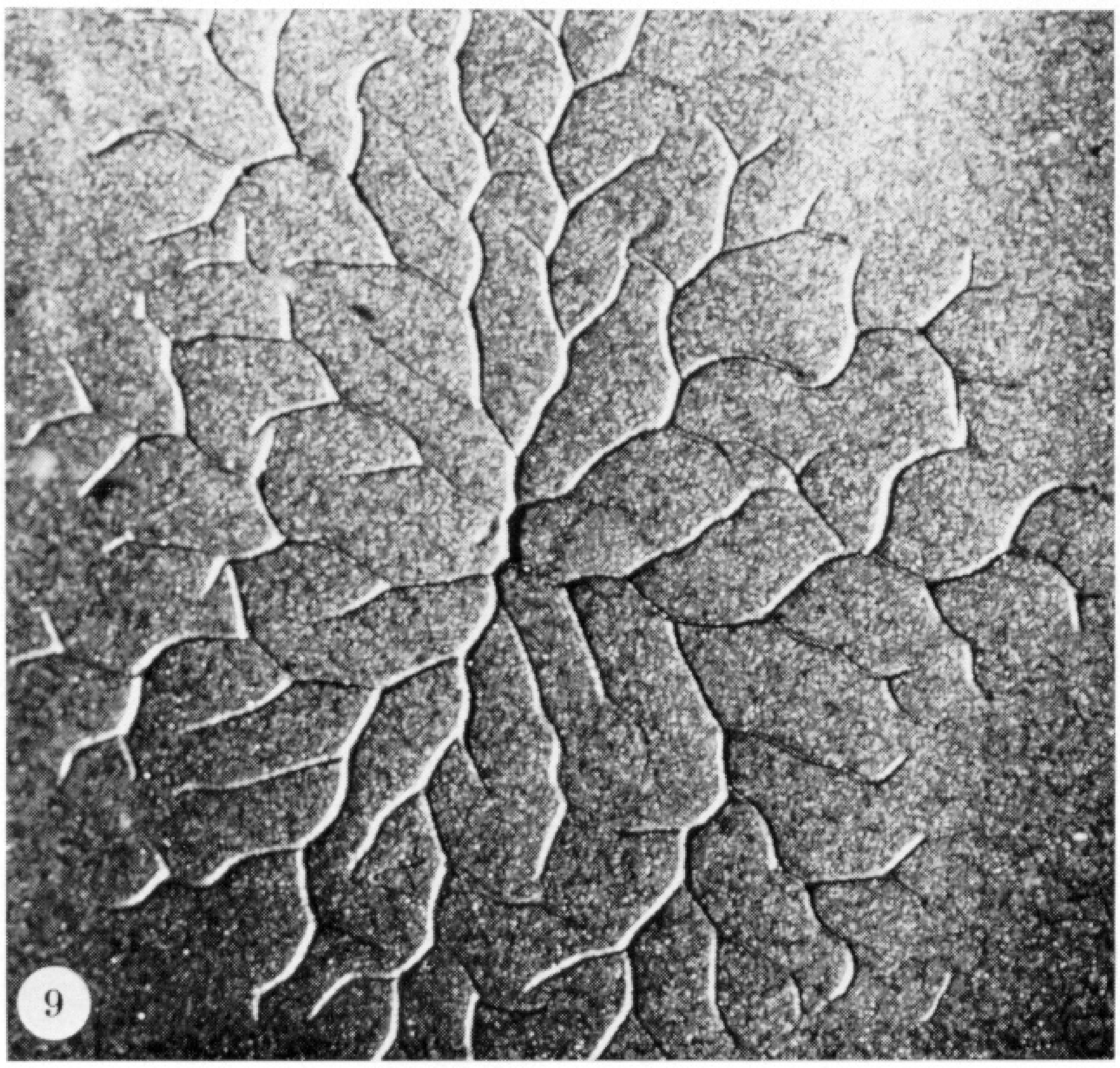
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FIGURES 4–9. For description see opposite.