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RECURRENT RED TIDES, A POSSIBLE ORIGIN OF THE SOLNHOFEN LIMESTONE. I

BY

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ABSTRACT

After a short description of characteristics, thanatocoenose and types of sediments, information is given on recent red tides and their effects. Although at present most authors agree that deposition took place under permanently marine conditions, there is less consensus of opinion with regard to the origin of the limestone. Extreme conditions during sedimentation and peculiarities of the fossilization all get a causal connection when recurrent red tides, predominantly caused by Coccolithophoridae, are assumed for the Solnhofen area. The assumption of recurrent red tides, considered responsible for the sudden death of nekton in surface waters and also seen as the origin of the lime-mud that rapidly covered the just killed macro-organisms, is elaborated in a reconstruction of the paleoecology.

SOME CHARACTERISTICS OF THE SOLNHOFEN LIMESTONE

Although the Solnhofen Limestone is extremely poor in macrofossils, mainly of marine origin, the extremely high standard of preservation even of very fragile organisms such as insects, caused much attention to be paid both to the fossils themselves, as well as to the mode of preservation.

Fossils are almost exclusively found on or near the beddingplanes of the well-layered limestone and throughout the centuries workers in the quarries looked at several hundreds of square kilometres of sediment-surface.

At present it is generally accepted that the high standard of preservation of macrofossils was caused by rapid sedimentation of lime-mud during or immediately after death of the macro-organisms. Less well preserved macrofossils with bones or scales lying in scattered groups, give indication that in most places near the sediment surface bottom currents were weak or absent and that decomposition mainly took place under anaerobic circumstances. Benthos is almost completely absent and most macrofossils belong to free swimming organisms.

ABEL (1927), one of the most outstanding authors during the early part of this century, advocated the theory that deposition of the limestone took place under lagoonal conditions, behind a barrier reef, and that periodically withdrawal of seawater from the lagoonal flat caused the death of marine macro-organisms.

Although some authors still adhere to the theory of Abel, sometimes with minor variations (MAYR, 1967), several other authors rejected the lagoonal heory and supported the conception that deposition took place under permanently marine conditions. The lethal conditions near the sediment surface throughout the deposition of the limestone could be attributed to the fact that the limestone was deposited in basins, situated between dead reefs, and also to the stagnancy of seawater in the lower, central parts of these basins.

Geologically the Solnhofen Limestone is not sharply defined, the limestone being of a special facies, occurring during the Malm ζ 2a, 2b and 3 (FESEFELDT, 1962) in restricted parts of a large area of about 10 by 60 kilometres (from east to west) between Daiting, Solnhofen and Kelheim. Other limestone deposits of nearly the same facies and age occur outside the Solnhofen area, but are at present excluded from the Solnhofen Limestone proper.

In previous literature the Solnhofen Limestone was less sharply defined, which means that faunal lists, as for instance that of WALTHER (1904), are only partly correct when one considers the modern definition of the Solnhofen Limestone, In this publication the conceptions of Fesefeldt are followed.

One of the most important features of the Solnhofen Limestone is the extremely good layering. Each limestone layer, with an individual thickness varying from a few millimetres to about 30 centimetres, with an average of about 2 centimetres, is separated from the adjacent layers by a very thin, marly intercalation. Beds which provide plates of good quality are called "Flinz"; the marly intercalations or series of limestone-beds either too thin or too weak to exploit, are thrown away and are called "Fäule".

Although there are minor changes in faunal content and also small variations in the admixtures of erosional products, the rather regular alternation of limestone beds and thin marly intercalations went on throughout Malm ζ 2a, 2b and 3.

Only two times this rhythmic sedimentation was interrupted: at the end of the Malm ζ 2a a submarine slide occurred in the Solnhofen area and a second slide of the same character took place at the end of the Malm ζ 2b. In both cases the material picked up in these slides, was of the same type as the preceding, well layered limestones. At present the sliding material forms two series, each a few metres in thickness and consisting of strongly convolute limestone beds, resting almost without any truncation on top of the undisturbed deposits.

Both during the sedimentation of the Malm ζ 2a, as well as during the Malm ζ 2b, reef swells were "en relief" and protruded slightly above the sediment-surface. Individual limestone beds are at their thickest near the central parts of the basins and thin out near the reef swells. On top of the reef swells only "Fäule" are present, thin limestone beds alternating with marly layers, the last mentioned layers forming the thin intercalations between the limestone beds in the central parts of the basins.

From observation of macrofossils it is inferred that the limestone beds underwent strong compaction after deposition (BARTHEL 1964, MAYER 1966, VAN STRAATEN 1971). Calculations give a compaction-factor, varying between 4 and 6, which means that a limestone bed with a present thickness of 2 cm was originally a bed of 8 to 12 cm in thickness. MAYER (1966) also mentions the fact, that in the immediate vicinity of large macrofossils (*Pleurosaurus*; *Caturus*) the limestone layers still maintain their original thickness, whereas the same layers some distance away from the fossil show the effects of compaction resulting in one fourth or one sixth of the original thickness.

MAYER (1966) shows that decomposition-products of the decaying organisms caused a rapid consolidation of the lime-mud both above as well as below the organism. In the case of the *Pleurosaurus* up to seven limestone layers above the fossil are affected by the above mentioned process, which means that these layers were already deposited above the dead organism when the decomposition of the organism was still incomplete.

In my opinion two conclusions may be drawn: the sedimentation of the limestone layers was rather rapid and/or the decomposition of macrofossils was rather a slow process. Moreover the conclusion seems justified, that compaction mainly took place some distance away from the sediment surface, when several different layers of lime-mud were already present. This opinion is not in conflict with the supposition of JANICKE (1969) who thinks that each layer already showed effects of compaction when the next layer of lime-mud was deposited. Compaction is always a continuous process, starting immediately when sediment is deposited. Moreover, as will be discussed later in this publication, there are strong indications that depostition of lime-mud occurred rather rapidly and was followed by a relatively long period during which the thin, marly intercalation was deposited, some compaction of the lime-mud layer having already taken place before the next layer of lime-mud was deposited.

During the above mentioned period before the next layer of lime-mud was deposited, the surface of the previous deposit of lime-mud also acquired its peculiar topsurface: a rather rough surface with slightly sunken areas, separated by anastomizing, sharply protruding rims. These rough topsurfaces were previously seen as mudcracks (SCHWERTSCHLAGER 1919, MAYR 1967) but are now mostly considered to be the result of socalled "syneresis", subaquatic expulsion of solvents from a gel. That these rough topsurfaces were already present, when the next layer of lime-mud was deposited, is clearly demonstrated by the following observation:

During a visit to the great municipal quarry of Solnhofen a rather poorly preserved fish (*Leptolepis* cf. *knorri* Ag.) was visible on the topsurface of one of the bedding planes at the end of a long stretch of about 10 metres, and 30 centimetres in width, where several imprints of the fish were visible and the normal rough topsurface of the limestone layer was completely wiped out. (Fig. 1.) Scales of the fish were strewn over the area, indicating that the imprints were made when the fish was already dead, the erased rough topsurface indicating that this rough surface was already present when the dead fish entered the sedimentation-area.

Such rough topsurfaces are readily casted by the underside of the next lime-mud deposit, as is also demonstrated by the excellent preservation of Limulid-tracks, visible both on top of the underlying limestone layer, as well as on the underside of the following limestone deposit.

The rough top surfaces and the subsequently formed casts on the underside of the next layers — the last mentioned surfaces having a soft texture due to small, slightly raised areas, separated by grooves — are possibly, and in that case erroneously, interpreted by VAN STRAATEN (1971) as load casts.

The rough top surfaces and soft-textured undersides of limestone layers are a good top-bottom criterium when the original position of a plate must be ascertained later on, when already removed from the quarry.

Another good top-bottom criterium is afforded by most macrofossils themselves. Nearly all macrofossils are found on the boundary between two successive limestone layers, often more or less sunken into the underside of the limestone layer that overlies the fossil. Especially ammonites, but also well preserved fish, shrimps and squids are found a little above the boundary plane between two limestone layers, slightly sunken into the underside of the toplayer and more or less elevated on top of a so-called "socle", protruding from the topsurface of the underlying limestone layer.

These peculiar socles underneath the well-preserved fossils were previously seen to be the result of an upward movement of the dead organisms during the first stages of compaction accompanied by increase in density of the surrounding sediment (ROTHPLETZ, 1909).

Today most authors consider the formation of socles to be the result of the sedimentary process during which lime-mud not only covered the macrofossils but also filled the empty spaces underneath the sides of ammonites and fish still posssesing their original shape. Subsequent compaction, together with a strong reduction of the vertical dimensions of the decaying organisms caused by slow downward movement of lime-mud above the organism and a slow upward movement of underlying lime-mud, led to formation of the socle and the sunken position of the fossil in the underside of the overlying limestone layer.

In the case of fossil fish lying on a socle, the paired fins and especially the caudal fin are usually not involved in the process of socle formation. They have a slightly inclined position, bending down from the sides of the socle to the top surface of the underlying sediment, thus indicating that the fish was resting on the boundary plane at the top of the underlying limestone deposit before the next layer of lime-mud was deposited.

Although a socle is not present when fossils are embedded in the so-called "Fäule" (JANICKE, 1969) nor when the dead organisms underwent strong decomposition prior to being covered by the next lime-mud deposition, skeletal material of the original organisms, such as bones or scales, adhere in most cases to the underside of the overlying sediment.

When examining fossil ammonites it is seen that they often contain the aptychi or synaptychi, lying somewhere near the entrance of the living chamber, and that sediment only seldom entered the living chamber. In most cases the sides of the ammonite are completely pressed together and dissolved, the aptychi or anaptychi however are not dissolved and lie in the plane of sedimentary surfaces. Ammonites, mostly broad types with strong spines, are nor infrequently found in a vertical position in relation to the sediment surface. They are often compressed to one-fourth or one-sixth of their original vertical dimensions. In exceptionally few cases, and only in connection with large specimens of ammonites, an oblong impression of the keel of the living chamber can be observed in the immediate vicinity of the horizontally embedded specimen.

The ammonite had been resting on the sea bottom in a vertical position for a considerable time with the living chamber at the underside, long enough to make an impression in the lime-mud. Suddenly it came into a horizontal position and was subsequently covered by the next lime-mud deposition. Ammonites with an impression of the keel near the living chamber were considered by ABEL (1927) and MAYR (1967) as an supporting evidence for the lagoonal theory; when seawater withdrew from the lagoon the ammonite came to rest on the bottom and when seawater was completely withdrawn the ammonite moved into a horizontal position. Today most authors prefer the theory that seawater was constantly present in the Solnhofen area and the above mentioned ammonites with keel impression are considered as evidence of extremely quiet conditions near the sea-bottom.

As indicated above, macrofossils are almost exclusively found on the bedding planes between two successive limestone layers. Only very seldom are macrofossils found embedded within the limestones. Although WALTHER (1904) stated that macrofossils exclusively occur at the boundary between two limestone layers, present large collections sometimes possess a few, very rare fossils that are embedded within the limestone layer. After periods of frost, fragments of massive limestone sometimes splits open revealing an embedded fossil. According to MAYER (1967) most fossil specimens of jelly-fish are found in this way.

THE SOLNHOFEN THANATOCOENOSE

Back in 1891 von Gümbel gave an impressive list of all macrofossils found in the Solnhofen area, followed by a list of Walther in 1904. Several of Walther's "species" later proved to be synonymous and he mentioned fossils found in deposits, not included in the Solnhofen Limestone proper. KUHN (1971) mentions about 700 species of macrofossils.

In 1967 Groisz added 24 species of foraminifera, found in marls of the

Malm ζ 2a, and further 60 species of foraminifera from the Malm ζ 2b, to the four species mentioned by WALTHER (1904).

FLÜGEL & FRANZ (1967) mentioned the presence of Coccoliths, showing a resemblance with the genus *Colvillea,* found with the aid of electronmicroscopic investigation of the Solnhofen Limestone.

Considered as a whole the thanatocoenose may be divided into three groups:

a. *Marine, free swimming organisms*

To this group belongs the majority of all fossils. According to VAN STRAATEN (1971) even 99,99 % of all fossils belong to free swimming organisms. *Saccocoma pectinata* Goldf., a pelagic crinoid, normally in deposits of the Tethys, is the most commonly found macrofossil in almost all quarries. Arranged according to diminishing frequency the following list may be given: ammonites, fish, crustacea, squids and belemnites, reptiles.

Jelly-fish, often excellently preserved, are usually found in a restricted area near Pfalzpaint. The extreme conditions that have been responsible for their fossilization raised a lot of discussion as to whether they fossilized under lagoonal, partly subaeric conditions or under full-marine circumstances. At present most authors are in favor of a marine preservation by rapid sedimentary processes, followed by subsequent dehydration of the animal tissues. When considering the fossil fish, special attention must be paid to the fact that species of oblong shape, such as *Leptolepis sprattiformis* Ag., *Leptolepis knorri* Ag., and *Aspidorhynchus acutirostris* Ag. are often found in an odd, backwardly bent, horizontal position sometimes with the caudal fin twisted off from the rear of the body (MAYR, 1967). Several authors concluded that drying-up of dead fish after the withdrawal of seawater from lagoonal deposits was the only possible way to get such backwardly bent fossils. BARTHEL (1964, 1966) opposes this theory and is of the opinion that decomposition under sub-marine conditions can give the same results.

MAYR (1967), a keen observer, gives in his excellent publication "Paläobiologie und Stratinomie der Plattenkalke der Altmühlalb" not only examples of where, according to him, living fish made imprints on the bottom sediment, but also gives examples of "Aufsetzmarke", imprints near fossil fish, made by fish already dead. Mayr also states that these fish in several cases only rested with their head, or with a part of their back, on the bottom before they turned over and lay flat on the bottom. It is clear that in such cases the dead fish were already bent backward by forces, developed by decomposition, mainly in the region of the intestines.

In the case of fossils of *Aspidorhynchus acutirostris* Ag. one can quite often observe rather deep and sharp imprints near the upper part of the caudal fin and near the dorsal fin. The fish itself lying in a ventrally bent position. This means, that a dead specimen rested only with the two mentioned fins on and in the bottom sediment, whereas the body of the fish stood in a reversed, upright position.

Such observations may be easily compared with the above mentioned cases of large ammonites found together with the imprint of the keel. They stood for some time upright and dead on the bottom, making imprints and afterwards, — in my opinion because imprints of an intermediate position are completely lacking, — rapidly got their horizontal position on the bottom. Moreover such examples give proof of the absence of bottom currents, at least in the period between the deposition of the underlying and overlying lime-mud deposition.

Special attention must be paid to the remark of MAYR (1967), when discussing examples of living fish that may have made imprints on the bottom, he states: "All diese Tiere sind bereits mehr oder weniger stark zerfallen". The fact that these fossils are decomposed before the next lime-mud sediment covered them is a direct indication that some time had elapsed, sufficient for decomposition and in the case of complete absence of bottom currents, before the next lime-mud sedimentation took place.

Undisputed life activities of macrofossils are the cases, where tracks of *Mesolimulus walchi* (Desm.) or of *Mecochirus longimanus* Schloth. led to the fossil specimen. JANICKE (1969), BARTHEL (1970) and VAN STRAATEN (1971) all mention the fact that recent relatives of *Mesolimulus* and *Mecochirus* are resistent to rather extreme variations in temperature, oxygen content and salinity of their environment.

BARTHEL (1970) moreover says that *Mesolimulus*-tracks are in several cases more or less arranged in circles, indicating disorientation of the still living animal. Barthel thinks that lack of oxygen seems to be a reasonable cause of death! In all cases ecologic conditions near the bottom must have been rather extreme, as all indications of real benthonic life are absent.

Of great importance are the electron-microscopic investigations of FLÜGEL & FRANZ (1967). They affirmed the remarks of VON GÜMBEL (1891), who was of the opinion that the Solnhofen Limestone was originally deposited mainly as lime-mud ("Kalkschlamm"), because he found in some layers countless well-preserved Coccolith's.

The results of Flügel & Franz confirm that the Solnhofen Limestone is a so-called micrite with a grain size smaller than 3,5 mu. The mean grain size is 1 mu. Only 2 % has a grain size up to 6 mu.

The Solnhofen Limestone consists almost exclusively of fragments of Coccolith's and complete Coccolith's are rather rare. The Coccolith's are not recrystallized and the fragments clearly show their boundaries and form the euhedral components of the limestone.

The Coccolith's belong to the subgroup discolith's, and, according to the systematics of Deflandre belong to the Heliolithidae. They show much resemblance to the genus *Colvillea* (Black & Barnes). Another, less frequently occurring form may possibly be identified as *Ellipsagelosphaera lucasi* Noël.

The density of Coccolith's in the Solnhofen Limestone is estimated by Flügel & Franz as 500.000 per cubic millimetre.

As to the origin of these enormous quantities of Coccolith's, Flügel & Franz are of the opinion that they did not live in the Solnhofen region but were transported from elsewhere. They seldom occur in lagoonal circumstances but have a great range in habitat and are often encountered as drifting plankton, for instance in the Oslo Fjord.

According to Flügel & Franz they drifted into the Solnhofen area, possibly together with Radiolaria and other plankton, from the open sea.

b. *Marine benthonic organisms, both sessile and vagile*

Walther (1904) stated that sessile benthos are extremely rare in the deposits of Solnhofen Limestones, and that when fossils of sessile benthos are found, they are always torn loose from elsewhere and transported to the Solnhofen area, or transported by drifting objects.

Fragments of seaweed are not infrequently found over the whole Solnhofen area, but they are always exceptions. Their presence may be easily accounted for, by being torn loose from elsewhere and transported into the Solnhofen area. Mayr (1967) even mentions seven cases of pebbles, transported from elsewhere to the Solnhofen area by means of attached seaweed. Indications that seaweed really lived in the Solnhofen area are completely lacking.

The same arguments hold for the occurrence of sessile organisms, such as Pectinidae, Ostreidae and stalked Crinoidea. In some very rare cases several specimens of Pelecypods are found close together. They are always of one species and, as may be concluded from growth lines of the same ontogenetic stage. Their occurrence in heaps, but often with their left and right valves loose makes it highly plausible that they drifted into the area, clinging to some drifting object, but died near the bottom before they became embedded in the next limestone layer.

For vagile benthos — again rather exceptionally found in the Solnhofen deposits — modes of transport may have been the same as for sessile benthos.

In extremely rare cases Pelecypods are found at the end of a track made by the animal itself in the bottom sediment. The extreme scarceness of such cases, together with the observation that in "normal" marine sediments fossil tracks of Pelecypods are usual but fossil bivalves at the end of a track are almost unknown, renders the highly acceptable conclusion that such animals found their way to the bottom of the Solnhofen basins by some sort of abnormal transport. The toxic environment near the bottom soon caused their death, so that the trail and the dead specimen are found together.

When considered as a whole, it must be concluded that in the whole area of the Solnhofen Limestone deposits (with the possible exception of

Zandt) conditions near the seabottom during the Malm ζ 2a, 2b and 3 were almost constantly of lethal character.

Only in one quarry, the rather southernly peripherally situated quarry near Zandt, the conditions near the bottom may have been at least during some periods less lethal than elsewhere in the Solnhofen Limestone area. This quarry, well known for its extremely good preservation of several species of Crustacea (often their exuviae too!) is also known for the large quantilies of wel preserved Asterozoa, *Geocoma carinata* Goldf.

Not infrequently fossil specimens of these extremely fragile Asterozoa are found in a position with all arms in one direction or with three or four arms in one direction and two arms or one arm in an opposite direction. Previously such alignments were seen as the result of transportation of dead specimens in a current, but investigations of SCHÄFER (1962) make it more plausible that the arrangement of the arms of these always excellently preserved *Geocoma*'s are to be seen as crawling tracks of living animals, trying to escape sudden burial under lime-mud. WALTHER (1904) was of this opinion too, when he stated "Die von dort (Zandt) stammenden *Geocoma*-Platten zeigen ganz deutlich dasz durch eine plötzlich hereinbrechende Katastrophe, vielleicht wiederholt, das ganze Gewimmel der zierlichen Seesterne getötet und mit feinem Kalkschlamm überdeckt worden ist. Die Tierchen haben nicht vermocht, sich durch die bedeckende, 3–5 mm dicke Schlammschicht hindurchzuarbeiten, und sind so rasch gestorben, dasz grosze und kleine Individuen ohne Verletzung, ohne Spuren des Zerfalles fossil wurden."

Of special interest are the investigations of GROISZ (1967), who sampled the microfaunae from the marly intercalations (the "Fäule") in the Solnhofen area.

In the deposits of the Malm ζ 2a only small populations could be recovered from the marly samples. Groisz listed 24 species. One species — *Nodosaria corallina* Gümbel — could not be demonstrated in the overlying Malm ζ 2b deposits.

Species of *Marginulina* and *Lenticulina*, which are main constituents of marine faunae outside the Solnhofen area, were only sporadically present in the Solnhofen deposits. Other microfossils are: Radiolaria, sponge spicules, juvenile brachiopods, ostracods, echinoderm fragments, fish- and algal fragments.

In the Malm ζ 2b-deposits, foraminifera were less scarce: 60 species were found, mostly in great numbers. From two species — *Paalzowella feifeli feifeli* (Paalzow.) and *Trocholina conica* (Schlumb.) — Groisz states that they display phylogenetic shifting. In the younger parts of the Malm ζ 2b *Paalzowella* becomes more flattened, whereas *Trocholina*, rather flat in the lower part, becomes more swollen in samples taken stratigraphycally higher up in the sections.

Other microfossils are: Algae, echinoderm fragments, juvenile and immature specimens of brachiopods, gastropods and pelecypods, and bryozoa.

From the radiolaria, present throughout Malm ζ 2a, 2b and 3, Groisz draws the conclusion that reefs were present in the immediate neighbourhood of the Solnhofen area and that climatic conditions were sub-tropical or tropical.

Although Nodosariidae are the most commonly found foraminifera in the Solnhofen sections, and under recent circumstances are indicative of the deeper parts of theneritic zone and upper parts of the bathyal zone, Groisz is of the opinion that the *absence* of *Epistomina*-species and the *absence* of sculptured forms (both characteristic of deeper water), may be considered as an indication that the depth of the sea was not great, possibly about 30 metres.

Groisz also states, that during sedimentation there was no hypersalinity or surplus of H_2S near the seabottom and the lacking of macro-benthos is considered the result of the bottom sediment, being to fine to allow larger benthonic organisms to live on. The micro-benthos is according to Groisz autochthon, only due to small changes in the faunal composition giving some evidence, that conditions in the Solnhofen area were slightly aberrant from normal marine conditions.

Regarding the paleoecology, Groisz is of the opinion that the Solnhofen area stood in connection with open sea, but was as a whole more or less sheltered by reefs.

c. *Macrofossils of terrestrial origin*

Without the presence of extremely well preserved fossils of terrestrial habitat the Solnhofen Limestone would never have obtained its worldwide fame and renowned position in geological and paleontological literature.

Archaeopteryx lithographica von Meyer presently known from five specimens, the best one still being that of 1877, the several specimens of Pterodactyloidea such as *Pterodactylus*, *Germanodactylus*, *Ctenochasma*, *Gnathosaurus* and the long-tailed *Rhamphorhynchus* aroused worldwide interest.

During the last 175 years about hundred specimen of Pterodactyloidea have been recovered from the Solnhofen Limestone (Wellnhofer, 1970) and their fossilisation was often extremely good, even showing details of their wings and the presence of webs between the toes of the foot (Döderlein, 1929). Both adult as well as juvenile specimens of several species of Pterodactyloidea have been found and we know at present that these fragile animals "were able to pick their prey from the water surface in full flight" and were "capable of swimming also" (Wellnhofer, 1970 p. 125).

In several cases the specimens are found with a strong, backward distortion of the long neck. Wellnhofer and other authors still believe that these Pterodactyloidea met their death somewhere on land and afterwards mummified; they subsequently drifted into the Solnhofen area, sank to the bottom and further decomposed. This theory is in accordance with the paleogeographic situation: most of the Pterodactyloidea are found in the neighbourhood of Eichstätt, situated peripherally near the northern boundary of the Solnhofen area, in the proximity of the great landmass of central Germany rising in the north above sealevel during this period.

The Solnhofen Limestone is also renowned for the excellently preserved terrestrial insects. About 180 species are known, again mostly found in the vicinity of Eichstätt. Only two species may possibly have been endemic (Kuhn, 1971), all other insects being of terrestrial origin and brought into the marine sediments by wind action.

The fossil insects were seen by several authors as evidence supporting the lagoonal theory (Mayr, 1967) but Barthel (1964) is of the opinion that complete absence of any imprints in the vicinity of the fossil insects and the results of experiments with dead insects floating on the water surface and afterwards settling on the bottom all support the theory that seawater was constantly present in the Solnhofen basins and that temporary withdrawal of seawater was not at all necessary for the preservation of insects.

Landplants are as a whole rather exceptional. They belong mostly to species of Conifera and may have been transported to the Solnhofen area by wind and waves. In the deposits of the Malm ζ 3, landplants are found rather more frequently, together with other, sedimentological indications that erosion products could more easily reach the sedimentation area.

Animals of freshwater living environment or of a brackish habitat are never found in the Solnhofen Limestone (Walther, 1904) but small reptiles, such as *Homoeosaurus*, possibly transported from land to sea in the shape of a mummy, belong to the very rare terrestrial fossils.

The sediments

The sediments may be roughly divided into two different kinds:

a. The marly intercalations, so-called "Fäule", containing about 85 – 91 % $CaCO_3$, a MgO-content less than 1 % and minor quantities of clay minerals and traces of quartz.

b. The limestones, so-called "Flinze", composed almost exlusively of $CaCO_3$ (97 – 98 %) with minor quantities of clay and quartz.

According to Fesefeldt (1962) there are actually no sharp boundaries between the two kinds of sediments, all intergradations between "Flinze" and "Fäule" being present. Fesefeldt even proposes names for sediments other than the two principal kinds; for instance, where limestone beds become very thin and marly sediment becomes quantitatively of greater importance, such as found near the old reef swells.

On the other hand in the central parts of the basins the number of limestone layers increases and the marly intercalations between the limestone beds become quantitatively of less importance.

On top of the buried reef swells only thin deposits, some metres in thickness and almost exclusively consisting of marly sediment (Fesefeldt's so-called "Grundfäule") are present, whereas in the central parts of the basins several tens of metres consisting of the regularly layered limestones are deposited.

These thin deposits on top of the reefs are of the same age as the thick deposits in the central parts of the basins and Fesefeldt correctly concluded that for the deposition of a "Fäule" of a certain thickness much more time was required than for the sedimentation of a limestone layer of the same vertical dimension.

That a relatively long period was required for the deposition of the thin marly deposits between two successive limestone beds, was seen by Fesefeldt as the cause of the differences in state of preservation of macrofossils.

In some cases organisms were shortly after their death rapidly covered by lime-mud, in other cases the dead organisms rested freely for a much longer period on the sediment, and thus were strongly attacked by decomposition and only afterwards were embedded by the next swift sedimentation of lime-mud.

As already mentioned, the mode of fossilization of some fossils, first standing upright on the sediment for a certain period and afterwards turned over in a horizontal position immediately beside the imprint made previously, give clear evidence of complete absence of or only very slight presence of bottom currents.

That in some cases bottom currents existed is demonstrated by "Roll-marks", a rather rectilinear series of oblong imprints made by the keel of ammonites, drag-marks of dead jelly-fish and other marks left by objects transported near or over the sediment surface. No proof of the existenc of really strong currents is ever found, and all effects one would expect to find when lagoonal conditions reigned during sedimentation of the limestones, such as wave or current ripples, mud cracks, cross-bedding, wash-outs and layers of coarse (organo) clastic material are absent (Van Straaten, 1971), possibly the only exceptions being the "ripple-marks" and drag-marks found in quarries near Pfalzpaint, Daiting and Painten (Janicke, 1969).

Save for the above mentioned exceptions, the layering of the limestone beds is extremely good: even thin beds of limestone can be traced over distances of three kilometres or more, and in several quarries or series of adjacent quarries, local names are given to certain parts of the sections worth exploitation, or those parts that on the contrary are useless and must be put aside before, lower situated, good "Flinze" are met.

Red tides. Recent observations.

"Red tide" or "red water" is the name given to seawater, discolored by the presence of large numbers of dinoflagellates in a density which is fatal to many forms of marine life.

Barnes (1966) states that during such outbreaks of red tide theoncentrations of metabolic substances reach such a high level that othec marine life is killed. During the red tide of 1948 near Florida millions of fish, crabs, shrimp and other animals were killed and the water acquired an oily yellow appearance.

Brongersma-Sanders (1948), who thoroughly investigated the phenomenon of red tide, makes a large number of observations and also gives a penetrating study on the causes of such red tides. The reader is referred to the paper of Brongersma-Sanders, but for convenience, some information will be given here.

Red tides only occur in certain regions of the oceans, where special conditions allow the outbreaks of this phenomenon. One of these conditions is the presence of upwelling seawater, rich in nutrients, combined — at least during part of the year — with a sufficiently high temperature near the surface.

Red tides especially occur in regions of upwelling seawater, situated along coasts where the wind is constantly blowing in the direction of the open sea, so mostly along coasts where a trade-wind or monsoon at least during part of the year is blowing from land to open sea. The most important areas, in this respect, are the west coasts of South Africa, South America, northwest Africa and California. Regions of upwell are also situated in restricted areas of the Caspian Sea and the Red Sea and in some cases upwell also occurs where submarine ridges cause bottom currents to deflect upwards or where divergences of surface currents cause deeper water to rise to the surface. Convection may also play a role.

The upwelling seawater, coming from depths of between 200 and 300 metres, is fairly cold and relatively rich in nutrients; mainly phosphates and nitrates. The upwelling water is of great influence on the climate of the hinterland.

Especially during the summertime the upwelling seawater is heated during its transport by trade-wind or monsoon from the original nearshore position to open sea. Possibilities for the occurrence of red tides are therefore optimal during the summertime and in several areas they occur every year.

Along the southwest coast of Africa there exists almost the whole year long a constant north-west wind, blowing obliquely to the coast and in a seaward direction. Although upwell is present the whole year long, upwell is less strong during December and January and the cold water coming to the surface along the shore is strongly heated on its way along the surface to the open sea (the southern summer!), where at a distance of about 400 miles from the coast the water goes down to a depth of about 80 to 100 metres and mixes with water coming upward at that depth from a still deeper level on its way to the shore.

The upwelling seawater, rich in phosphates and nitrates, being heated to temperatures of 16° or 17° C., together with the penetrating sunlight, makes ideal conditions for the phytoplankton to live on.

In most cases only one species of the phytoplankton rapidly increases in number and to such an extent, that not only all other phytoplankton are outnumbered, but conditions for all other marine life become lethal. Overdoses of metabolic substances from the plankton-species causing the red tide, and lack of free oxygen kill all other marine organisms. At last the species of plankton responsible for the red tide is also involved in the mass mortality.

Taking all the oceans into consideration, not always the same species of phytoplankton are the cause of red tides but in most cases they belong to some species of Diatomea or Dinoflagellata.

The effects of the red tide are downright disastrous. The first effect of poisoning is to make the fish sluggish and both juvenile and mature specimens of all species present in the area are thrown on the coast both alive and dead. When the toxic effect increases, for instance during days of calm weather and high temperature, fish die in great numbers, near the coast as well as in open sea. At first the benthonic fish are killed, later on the pelagic fish die. Not only fish are killed: Crustacea, Mollusca and Alcyonaria are also included in the mass mortality. During the almost annually occurring red tide along the southwest coast of Africa near the Walvis-Bay, ramparts of several metres high and almost exclusively consisting of dead fish are present on the coast and the air, being polluted by great quantities of H_2S, even causes houses or ships, normally painted white, to turn black!

But the effects of the mass mortality proceed: great numbers of birds are killed too and even seals cannot escape their fate.

On the seabottom the effects are possibly still more disastrous. Along the coast of southwest Africa, between 21° 30′ S. and 24° 30′ S., over a distance of about 200 miles the bottom sediments belong to an azoic zone. This zone stretches for a distance of 25 or 30 miles from the shore. In the zone the yearly occurrence of red tide has killed all benthos, only near the outer seaward limit, at a depth of about 160 metres, foraminifera and some mollusca are constantly trying to regain their lost territory.

The slowly moving benthos never enters the deadly azoic region; only their free swimming or pelagic larval stadia may enter, but they are killed during the next years outbreak of red tide, or are immediately killed near the toxic bottom-sediments.

The red tide itself only lasts for a few days, exceptionally a few weeks or a month, but near the seabottom large amounts of dead organic material are concentrated, rendering conditions both within as well as above the sediment toxic the whole year round. The sediment, and sometimes the seawater above the sediment too, contains a high percentage of H_2S and is almost or completely devoid of oxygen.

Other peculiarities of the bottom sediment in azoic regions are the abundance of fish-remains and sometimes the presence of a gelatinous mass, consisting of dinoflagellates that died shortly after the plankton maximum near the surface.

In particular the mode of decomposition of the fish is very curious. The relatively low temperature near the bottom, the absence of free oxygen, the complete absence of scavengers and the blanketing effect of the dead dinoflagellates are responsible for a mode of decomposition totally different from the normal process of decomposition. FALKE (1939) reported that several months after the occurrence of red tide in the Bay of Talcahuano, Chili, complete fish were hauled from the seabottom: "zuweilen wurden auch mit dem Schlamm gröszere, zusammenhängende Fischreste, die eine seifig-fettige Masse bildeten, ans Tagelicht gehoben, ja manchmal sogar vollkommen erhaltene Fischleichen noch Wochen und Monate nach dem groszen Fischsterben".

Such a decomposition under complete absence of oxygen means that not only fatty substances of dead organisms but also the muscles are converted into a rather rigid, soapy mass, called adipocere. Grave-diggers are well aware of this effect. Especially when human bodies were buried beneath the watertable — rather often the case in the polders of the Netherlands! — anaerobic circumstances were responsible for the preservation even of the facial expression over several tens of years!

In areas where red tides occur yearly or almost yearly, the accumulation of organic material on the seabottom is abnormally high, aerobic organisms are almost absent and the decomposition, by anaerobic bacteria only, proceeds rather slowly. H_2S is constantly produced by the anaerobic, sulphate-reducing bacteria and decomposition, for instance of fish, may take several years or even more. Possibilities for benthonic organisms keep lethal constantly and only pelagic larvae may be encountered in the sediment.

The upwelling of cold seawater near the shore has a great influence on the climate. The humidity is often great, but rainfall in the areas inland is almost completely absent the whole year. In the case of southwest Africa a stretch of some 60 to 100 km wide, parallel to the coast, gets no rainfall at all although fog may occur. The riverbeds are dry almost the whole year long and only contain some water when rainfall occurs far in the hinterland.

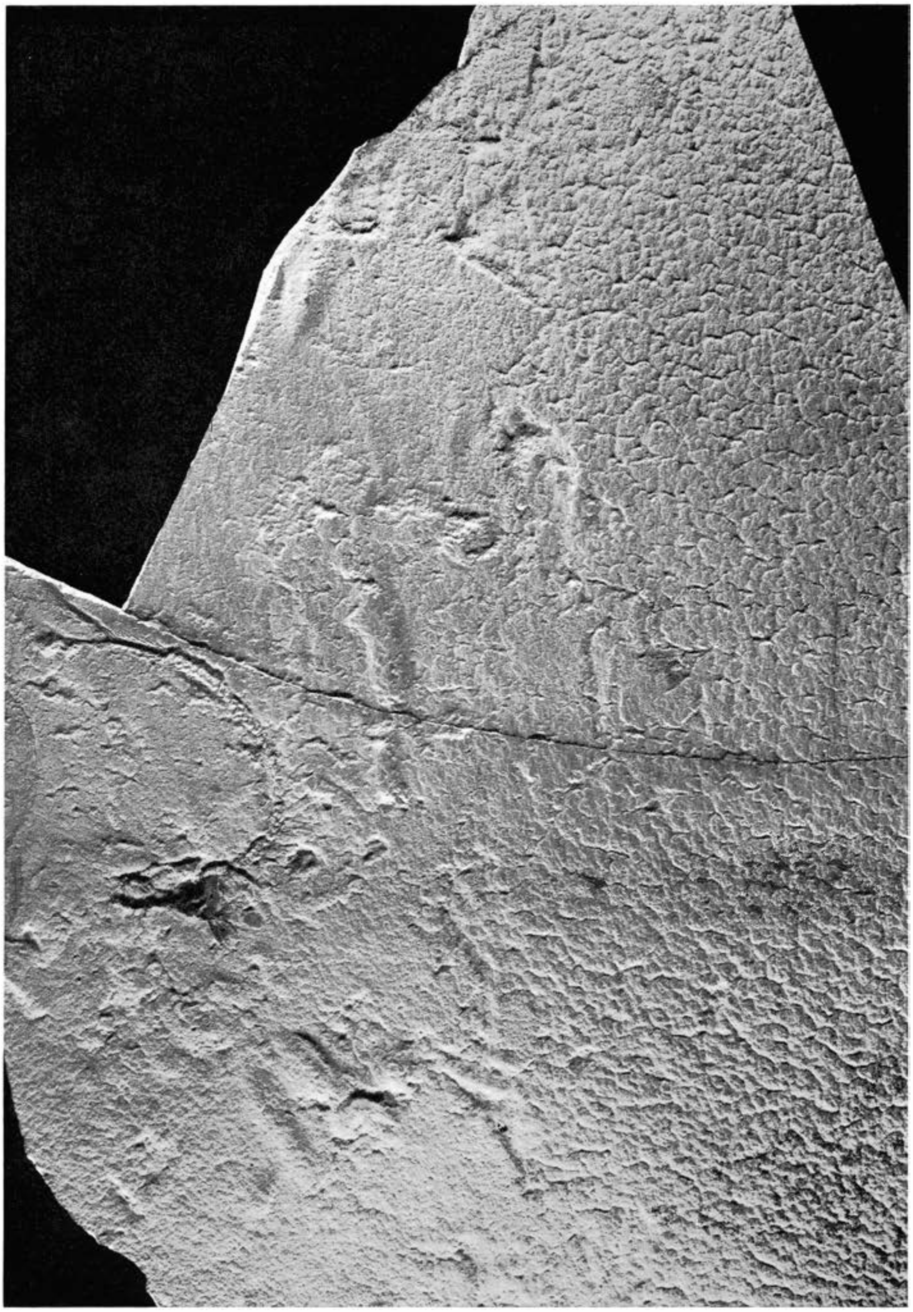

Fig. 1. *Leptolepis* cf. *knorri* Ag. (× 1/3). Municipal quarry, Solnhofen. Malm ζ 2b. Bottom sediments had already acquired the rough textured surface (visible on the right hand side), when the dead and slowly decomposing fish made several imprints on the sea bottom. Note the detached pelvic fins lying near the boundary of the rough textured sediment surface. View at the underside of the overlying limestone layer.

Fig. 2. *Thrissops formosus* Ag. ($\times$ 3/4). Wintershof near Eichstätt. Malm ζ 2b. A dead specimen, strongly bent backwardly, rested with the abdominal region on the sea bottom, whereas buoyancy held the front region and head of the fish in an upright, vertical position. When the fish turned over in a horizontal position, the caudal fin, being more or less anchored in the sediment, was torn loose from the rest of the body. Note the different level of the two tips of the caudal fin. View at the underside of the overlying limestone layer.

GEOLOGY

RECURRENT RED TIDES, A POSSIBLE ORIGIN OF THE SOLNHOFEN LIMESTONE. II

BY

P. H. DE BUISONJÉ

(Communicated by Prof. H. A. BROUWER at the meeting of September 25, 1971)

ORIGIN OF THE SOLNHOFEN SEDIMENTS

Although the lagoonal theory of ABEL (1927) is discarded nowadays by most authors (KUHN, 1971), the origin of the lime-mud and the more marly intercalations is still uncertain, even for those authors who are convinced that sedimentation took place constantly under marine circumstances.

VON GÜMBEL (1891) was of the opinion that the lime-mud consisted for the greater part of Coccoliths and his conception was only confirmed by Flügel & Franz in 1967.

WALTHER (1904) thought that the — lagoonal — sediment consisted of dust, blown from land into the lagoon and that the lime-mud was derived from nearby situated dead reefs.

ROTHPLETZ (1909) stated that the sediment was derived from land, transported by wind, and afterwards transformed into mud by invasions of the sea.

ABEL (1927) was also of the opinion that the sediment was blown into the Solnhofen area from land, but KRUMBECK (1928) was more or less of the same opinion as VON GÜMBEL (1891) and thought that the sediment was of marine origin.

DEHM (1956) thinks that the lime-mud is derived from micro-organisms, wether animal or vegetable, their fossils being destroyed by decomposition.

FESEFELDT (1962), when discussing the origin of small quantities of quartz, with a mean grainsize of 25 mu, and occurring in limestones, slightly younger than the Solnhofen Limestone proper but of nearly the same sedimentological character, states that this material is derived from land. Fesefeldt denies the possibility that this material is of fluviatile origin and thinks that dust storms were responsible for the deposition and that aride climatic conditions prevailed on land: "Aus dem Staub auf ein Festland mit aridem Klima zu schlieszen ist erlaubt".

MAYR (1967) points to the possibility that lime-mud may be deposited chemically or bio-chemically, together with lime-mud derived from nearby situated reefs.

FLÜGEL & FRANZ (1967) are of the opinion that the lime-mud originated from drifting masses of plankton, entering the Solnhofen sedimentation area.

JANICKE (1969) makes a sharp difference between conditions during sedimentation of "Fäule" and "Flinze" and thinks that changing waterlevels in very flat lagoons are responsible.

VAN STRAATEN (1971) is of the opinion that chemical sedimentation from seawater is impossible and that the lime-mud is deposited from suspension, the suspension being caused by heavy storms that stirred up carbonate mud deposited in a very shallow sea, north of the present Solnhofen area. The more marly "Fäule" are according to Van Straaten derived from land and transported during periods of rainfall in the fresh water spreading over the sea.

When discussing the origin of the sediments a number of observations and conclusions must be kept clearly in mind:

1. Macrofossils belong almost exlusively to free swimming types. They belong to the sedimentation periods of the marly intercalations, the so-called "Fäule".

2. Benthonic macrofossils, especially of slow moving or sessile types are almost completely absent, both in the "Fäule" as well as in the "Flinze". Their absence indicates that lethal, anaerobic conditions, not only in the sediments but also in seawater near the sediment surface, were almost constantly present during sedimentation of the Solnhofen Limestone.

3. The "Fäule", wether deposited as rather thick marly limestones on top of dead reef swells or as very thin intercalations between successive limestone beds are the *normal* sediments in the Solnhofen area. They consist partly of carbonate, mostly derived from pelagic organisms and deposited from very slow moving currents or descending from the surface, partly of clay and very fine quartz, derived from land situated north of the Solnhofen area and brought into the sedimentation area by wind, possibly blowing more or less constantly from that direction.

4. The "Flinze", deposited as rather thick layers of lime-mud, containing a high percentage of fluid and only afterwards showing effects of a rather strong compaction, are the *abnormal* sediments. The limestone beds are almost devoid of both macro- and micro-organisms, except for enormous quantities of Coccoliths. Other faunal elements and also clay- and quartz-admixtures being almost completely absent, one may draw the conclusion that sedimentation of the lime-mud took, place in a rather short time as compared with the deposition of the "Fäule" and was of *abnormal* biochemical origin.

5. Macrofossils may be subdivided, according to their state of preservation into three different types: one type being always excellently preserved but with strong effects of vertical compaction, indicating that the dead organisms were rapidly covered with sediment. The second type always shows effects of rather strong decomposition under anaerobic circumstances and under absence of strong bottom currents. In such cases all skeletal elements of the organism are lying close together, either in

their original position in the organism, or scattered over very short distances. In the third type of preservation only fragments of organisms are present, for instance the bones of a fish-head are found all in original position, but from the backbone only the first vertebrae are present. Tail-fins, together with the last few vertebrae are also well-known as fossils and fossils consisting for instance of all the bones from only one wing of a Pterodactyloid also belong to this type. Here there are indications that dead macro-organisms first floated for some time near the surface and fell apart, but when such fragments reached the bottom they escaped further disintegration into single bones, all bones still in their original position lying together.

6. The normal sediments, the "Fäule", containing only immature specimens of sessile, benthonic organisms wit a life-cyclus of more than a year, the abnormal sediments, the "Flinze", occurring repeatedly and rather regularly in all vertical sections of the Solnhofen Limestone, lead to the conclusion that the short periods of "abnormal" sedimentation are recurrent seasonal effects, occurring once a year or once in a few years.

7. Stagnancy of seawater near the seabottom, must be assumed for the whole region of the present Solnhofen Limestone, not only for individual smaller basins, but also for the higher situated reef swells separating these basins.

Reconstruction of the paleoecology

During the Malm δ, ε and part of the Malm ζ, reefgrowth, mainly of sponge- and algal-reefs, occurred not only in the region where later on the Solnhofen Limestones were deposited, but also outside this region.

This reefgrowth occurred only along certain parts of the seabottom, along more or less north-south lying reef tracts or reef-swells, separated by basins. In these basins no reefgrowth occurred and here the mostly fine detritic materials, derived from nearby living reefs, were deposited.

At the onset of the Malm ζ 2a, the situation suddenly changed. All reefgrowth stopped, even on top of reefs, situated at different topographic levels, at least in the area of the later Solnhofen Limestone. Outside the Solnhofen area the reefgrowth went on uninterruptedly.

The cause of the sudden change in conditions is still not clear; the sediments of the Malm ζ 2a are of the typical Solnhofen character; thin marly beds alternating with pure limestone, but they still contain some fine detritus, derived from limestone elsewhere (Fesefeldt, 1962). The sediments of the Malm ζ 2a gradually filled the basins and relatively thin deposits also covered several reef swells.

At this time a deposit of a submarine slide ("Trennende Krumme Lage"), composed of the same sediments as deposited previously, occurred in the Solnhofen area. This slide was possibly triggered by a regional tectonic event, and after this slide typical Solnhofen limestones were deposited again, concordant with the top of the slide.

Sediments of the now following Malm ζ 2b are completely devoid of detritus, such as was still present in the preceding Malm ζ 2a.

After the occurrence of a second submarine slide of the same type as the first ("Hangende Krumme Lage"), again conditions slightly changed, and the now following Malm ζ 3, although being of the typical Solnhofen character, again shows influx of detritic materials, together with minor changes in the faunal composition.

Concerning the cause of the changing conditions within the Solnhofen area throughout Malm ζ 2a, 2b and 3, one is inclined to think that a combination of several independent events worked together. Slow tectonic rise of the hinterland in the north together with a downward movement of the region in the south, two submarine slides of regional character, changing positions of seawater currents, changing climatic conditions, especially in connection with the rising landmass in the north and adaptation of both sedimentological-morphological character as well as adaptation of reefs and other lime-secreting organisms may all have been of influence on the very special ecologic conditions that reigned during the deposition of the Solnhofen Limestone.

In the opinion of the author recurrent red tides in the Solnhofen Limestone area were responsible — apart from a special seabottom-morphology — for the extreme conditions, both with respect to the composition of the thanatocoenose and mode of fossilisation, as well as with respect to the sedimentation itself.

But, as was seen earlier in the description of recent red tides, the causes of these are of an intricate character, several factors working together and none of the individual factors being alone of influence on the outbreak of a red tide.

From the changing sedimentological character throughout the Malm ζ 2a, 2b and 3 it becomes clear, that minor changes in the admixture of small detritus did not influence the rhythmic alternation of "Fäule" and "Flinze".

When taking into consideration all possible evidences, the postulation of recurrent red tides seems justified. Paleontological observations and sedimentological investigations get a causal connection. Let us try to give a depiction of the recurrent events.

During the periods of normal sedimentation deposition of the "Fäule" took place and a trade-wind or monsoon, blowing constantly the whole year, or at least constantly during part of the year from the landmass situated north of the Solnhofen sea, transported fine dust, mainly of clay-minerals and very fine quartz into the area.

Normal surface water, probably to a depth of fifty or hundred metres, enabled free swimming macro-organisms such as ammonites, fish, shrimps and squids to enter and live in the Solnhofen area, living directly or indirectly on the phytoplankton, present too in the surface water. Pterodactyloidea, able to swim on the surface, were flying over the sea, probably living from small pelagic organisms.

Upwell of seawater, coming from rather great depth from the Tethys and rich in anorganic nutrients, occurred throughout the years in the Solnhofen Limestone area. This cold water coming to the surface near the shore of the great landmass in the north was heated and driven back to the south. Only during the mid-summer-period heating of surface water was strong enough to cause a red tide: from the ever present plankton one or two species — in this case of Coccolithophoridae — multiplied very rapidly and to such an extent that all other marine life was killed, surface water became temporarily almost devoid of oxygen, and finally the great masses of Coccolithophoridae, "responsible" for the red tide, were killed as well.

From this moment on the succession of events is plausible: macro-organisms, poisoned by the metabolic substances of the Coccolithophoridae, mostly went down to the bottom immediately because anaerobic decomposition took place, preventing long drifting or floating as is normally the case under aerobic circumstances. Immediately after the dead macro-organisms had reached the seabottom a thick jelly-like mass of dead Coccolithophoridae reached the bottom too. This mass contained still large quantities not only of seawater, but possibly also contained some oil, because other phytoplankton often has a droplet of oily substance within its membrane in order to permit equilibrance for its heavy exo-skeleton.

Rather soon, in some cases already next year or otherwise a few years later, the next lime-mud was deposited and compaction of the previous lime-mud was still not finished when the next layers were already deposited. Expelling of fluids from the lime-mud started immediately after deposition and caused the synerese-effect at the top-surface. But compaction still went on, and even layers of lime-mud covered by several others, still expelled water and some oil.

The morphology of the seabottom, together with the compaction of lime-mud in the depressions, was mainly responsible for the stagnancy of seawater near the bottom. Several smaller basins were present, and possibly all these smaller basins belonged to a much bigger basin or depression, larger than the present area of the Solnhofen Limestone.

Dead reef swells and probably the still living reefs outside the Solnhofen area too, permitted stagnancy of water near the bottom and even stagnancy over reef swells, projecting not to far above the level of adjacent smaller basins.

Stagnancy of bottom water, low temperature and the presence of great quantities of organic material, lack of free oxygen, presence of H_2S and possibly absence of penetrating sunlight, made that decomposition both of Coccolithophoridae as well as decomposition of macro-organisms was of anaerobic character.

Macro-organisms were transformed into rigid masses of adipocere, still possessing their original three-dimensional shape, and such very slowly decaying organisms — even when not covered immediately by lime-mud — were capable to rest nearly unaltered for several months on the seabottom without falling apart. Seen in this light, the imprints on limestone surfaces, previously explained as "life-activities" or "traces of death-struggle" can be easily accounted for. Bodies for instance of fish, transformed into adipocere, rested as such for months on the seabottom and made imprints into the top-surface of the underlying lime-mud. They were easily transported or translated even by very feeble currents or eddies because their total density was only slightly more than that of surrounding seawater. New imprints were made nearby, and at the end of such series of imprints, the skeleton of the macro-organism — mostly showing strong effects of decomposition (see page 158) — is found.

When dead fish were replaced by adipocere, slight upward forces caused by gas-pressure in the intestinal region of the slowly decomposing organism, were not only able to give the fish a backwardly bent shape, but also caused buoyancy of part of the fish enabling it to rest for some time in an upright position on the seabottom. A good example is given in fig. 2. where the caudal-fin is broken free from the rest of the fish. Here the front part of the fish had an upright position, the fish only resting with its abdominal region and the lower half of the caudal fin on the seabottom. When later the fish came into a horizontal position the caudal fin was torn loose, the two extremities of the caudal fin having a different level in the sticky sediment.

One of the most common fossil fish, *Leptolepis sprattiformis* Ag., is not infrequently found with its caudal fin torn loose from the rest of the fish. It is not impossible that buoyancy held these small fish for some length of time in a vertical position, resting only with the caudal fin on the bottom. When the fish came to rest horizontally during the next years lime-mud deposition, the caudal fin, already more or less anchored in the lime-mud, was disengaged from the rest of the body.

The supposition of recurrent red tides also gives a good explanation for the differences in preservation of macrofossils. Macro-organisms killed during a red tide and covered by the lime-mud, consisting of dead plankton of the very same red tide, gave excellently preserved fossils, afterwards pressed by compaction into their slightly sunken position into the undersurface of the limestone bed and resting on a socle underneath.

Macro-organisms killed during a period of red tide, but not covered by lime-mud of the very same red tide, kept lying free on the bottom, at least for one year or more. During this period the anaerobic decomposition went on slowly, and the organisms — under complete absence of strong currents and activities of scavengers — fell apart, all skeletal elements lying close together.

In other cases, when fish or other macro-organisms died during the period of normal sedimentation, also decomposition in oxygenated water near the surface took place. The fish's head region was mostly disengaged from the rest of the body. The complete wings of *Pterosauria* were also soon disengaged. When such fragmentary organisms reached the azoic region near the bottom, decomposition of an anaerobic type took over and all skeletal elements of the fragmentary organism kept together on the seabottom.

Also the very rare cases where fossil fish-of-prey are found with their prey partly swallowed, may be easily explained. During the first stages of the mass mortality fish became sluggish by poisoning, swallowed another victim of the poisoning, but were unable to digest their prey completely because they died themselves.

The presence of insects, previously seen as an argument in favor of the lagoonal theory, can be easily accounted for. MAYR (1967) states that in normal cases dead insects, floating on the surface are either eaten by fish or washed ashore by wind, But when red tides occurred there were no fish alive anymore and probably the direction of the wind was off-shore!

The same explanation also holds for the other fossils of terrestrial habitat. Pterodactyloidea either died on the surface of the sea or along the shore (WELLNHOFER, 1970 prefers the last possibility) and the off-shore wind could transport mummies of such animals over sea before they sunk to the bottom. In our picture they also died in some cases already at sea!

The fossilization of jelly-fish can be elucidated too. MAYR (1967) mentions that fossil jelly-fish are in most cases not found at the underside of the limestone beds, but within the limestones, especially when they are split open by frost.

It is clear that when jelly-fish were killed during a red tide and went down to the bottom together with great numbers of dead plankton, they were simultaneously covered with a jelly mass of lime-mud. The lime-mud effectively retards the decomposition of the jelly-fish and synerese of the lime-mud starts immediately after deposition, forming sharp casts of the tissues of the jelly-fish. In some cases shrinkage of the dead jelly-fish took place during the decomposition, possibly by expulsion of seawater from the animal tissues and concentric imprints were formed near the periphery of the jelly-fish.

In this connection it is also worth mentioning that according to MAYR (1967) most insects are found at the underside of the limestone beds, but also, and not infrequently, slightly higher up in the limestone, separated from the underside by a very thin film of carbonate. In our conception this would mean that most insects reached the bottom before the red tide, but some went down when it was on its maximum and dead plankton settled already on the bottom.

Due consideration must be given to the climatic conditions on land. For occurrence of red tides an important factor is the presence of a seawardly directed trade-wind or monsoon, in most cases combined with the presence of a desert along the shore. The complete absence of fossils from a fresh-water habitat is in close accordance with the supposition of a zone with aride conditions along the shore of the landmass north of the Solnhofen region. Small reptiles, although rare as fossils, are sometimes found in the Solnhofen Limestone and may be derived from the zone with aride climatic conditions, but landplants and above all specimens of *Archaeopteryx* — their habitat being situated still further landinward and rivers only exceptionally reaching open sea — will always stay extremely rare findings.

As for the climatic conditions considered as a whole, several authors mention a tropic or subtropic climate, but the present author would prefer a subtropic climate as most probably.

According to BRONGERSMA-SANDERS (1948) red tides mostly occur in regions just outside the tropics. In subtropical regions rather great yearly variations in temperature exist, whereas in tropical regions the supply of nutrients by upwelling seawater is mostly smaller and constantly consumed by phytoplankton because temperatures are relatively high the whole year long, preventing the occurrence of yearly red tides.

Concerning the depth of the sea during deposition of the Solnhofen Limestone only superficial information can be given.

In the first place it must be kept in mind that the Solnhofen Limestones together, including Malm ζ 2a, 2b and 3, have a total thickness of about 150 metres in the deepest parts of the basins and that there are no reasonable arguments to decide wether the whole area was tectonically stable during this period or not.

Only during the Malm ζ 3 there are sedimentological indications that erosional products, originating under near-shore conditions became more and more of influence on the sedimentation. This could point to a gradually decreasing depth of the sea.

On the other side GROISZ (1967) mentions that species of Nodosariidae are commonly found in the Fäule and according to POKORNY (1958) Nodosariidae are under recent circumstances typically for the upper part of the bathyal and the deeper part of the neritic zone, a depth of about 200 metres.

Such a depth would be in close accordance with data given on recent azoic bottom-zones. BRONGERSMA-SANDERS (1948) mentions the fact, that at the outer limit of the azoic zone near Walvis-Bay, South Africa, at a depth of about 160 metres, tests of foraminifera greatly increase in number and also empty shells of mollusca may be found. Here changing conditions temporarily permit benthos to re-enter the azoic zone.

Because there are vague indications that benthonic life was possible temporarily and for short periods, as is indicated by the foraminifera found by GROISZ (1967), and the observations of possible life-activities of *Geocoma* in the quarry of Zandt, and moreover deeper parts of sedimentary basins when attacked by subaerial erosion are more readily preserved than their marginal parts, it seems reasonable to place the Solnhofen Limestone deposits, especially those of Malm ζ 2b, near the outer limit of the original azoic zone, at a depth of about 200 metres. At the onset of deposition of the Malm ζ 2a, the depth in the central parts of basins will have been about

235 metres, during the deposition of the Malm ζ 3 about 150 metres.

During the Malm ζ 3 the depth gradually decreased and the influence of detritus, derived from near-shore became of importance. The deposits of the Malm ζ 3 are more or less wedge-shaped in north-south cross-section: only thin deposits overly the Malm ζ 2b near Solnhofen, whereas more to the south the deposits of the Malm ζ 3 reach their maximum thickness of about 70 metres.

During the Malm ζ 3 there is a sharp increase in the number of Radiolaria, present in the limestone beds. According to VAN STRAATEN (1971) some layers are true radiolarites.

Although radiolarites in recent times are seldom found close to the shore it is not impossible that slight changes in the morphology of the seabottom, upwelling of seawater still being present, also created favourable conditions for Radiolaria to live on. The supply of near-shore erosional products was still scarce when compared to the vertical supply of pelagica.

FLÜGEL & FRANZ (1967) mentioned a density of about 500.000 plates of Coccoliths per cubic millimetre. When calculated for a square piece of limestone with dimensions of 10 by 10 cm and 1 cm thick, the number of plates will be 5×10^{10}.

Now each Coccolithophoride has about 10 of such plates arranged on its celmembrane, so one centimetre of limestone sediment over an area of one square decimetre is derived from 5.10^9 living Coccolithophoridae. When the red tide occurred to a depth of about 100 metres from the surface, the density of Coccolithophoridae was about 5.10^6 per liter of seawater.

Such a density is in close accordance with the density for an outbreak of red tide in San Diego, California, mentioned by BRONGERSMA-SANDERS (1948), where 3.10^6 specimens of *Gonyaulax* sp. were found per liter during the red tide maximum.

It is clear, that when the red tide lasted for weeks or months lime-mud could accumulate to rather thick masses, after compaction building limestone beds of more than one cm in thickness.

Moreover, probably as a result of very slow density-currents, the thickness of the lime-mud deposits was not uniform. Near the central parts of the basins the lime-mud was deposited appreciably thicker than on top of the reef swells between the basins. (These slow density-currents are held responsible for the turning over of dead organisms that stood vertically on the sea bottom!).

As to the speed of sedimentation, it may be assumed that each limestone bed represents the deposit of one single red tide, but that it is not necessary that each marly intercalation represents only one single year, some of the "Fäule" being notably thicker than other marly intercalations. An estimation of about five or ten thousand limestone layers, deposited during the Malm ζ 2a, 2b and 3, and the red tides occurring not every year but with a mean frequency of about once every two to five years, the total duration of deposition will have been in the order of about 10.000 to 50.000 years.

The question, whether the thanatocoenose gives an exact picture of the biocoenose near the surface of the sea during the periods of normal, oxygenated and non-tonic seawater, must be denied. On the one hand proof is given that dead organisms, their habitat lying outside the Solnhofen area, drifted into the region and on the other hand it is known from observations on recent red tides that for instance shoals of fishes may escape the deadly region. But, although the thanatocoenose does not give a numerically correct picture, it certainly gives an excellent view on flora and fauna, not only immediately above the Solnhofen sedimentation area, but also on land and in the air.

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