PART A

INTRODUCTION

FOSSILIZATION (TAPHONOMY)
BIOGEOGRAPHY AND BIOSTRATIGRAPHY

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FOSSILIZATION (TAPHONOMY)[1]

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INTRODUCTION

The manner in which organisms become fossilized is one of the largest and most diverse areas of research in general paleontology. In essence, the concept of fossilization encompasses what Efremov (1940) called "taphonomy" (τάφος = burial, νόμος = law), which is the study of the transition of all or part of an organism, and its lebensspuren (ichnia), from the biosphere into the lithosphere. Taphonomy studies the introduction of the remains of organisms and their traces into the rock record.

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[1] Manuscript received October, 1973. This contribution was translated from the original German by W. G. Hakes and Curt Teichert.

> EFREMOV (1940, p. 85) originally defined the major concern of taphonomy to be "the study of the transition (in all details) of animal remains from the biosphere into the lithosphere, i.e., the study of a process in the upshot of which the organisms pass out of the different parts of the biosphere and, being fossilized, become part of the lithosphere."

Preservation is dependent upon the nature of the organism's body, biotope, rates of sedimentation, as well as the embedding medium; however, the real objects of study in taphonomy are biologic structures that are morphologically recognizable. Such studies are related to the destruction or preservation of an organism, and as a rule, proportionately very little of its entire mass will be preserved. Only the calcareous, siliceous, and chitinous hard parts stand much chance of preservation. The organic material eventually decomposes, becomes structureless, and is chemically altered, and the study of this organic material, which is known to influence the character of sediments, remains primarily the work of chemists, petrographers, and geologists.

Probably the first definition of the concept of fossilization was presented by D'ORBIGNY (1849):

> The term fossilization is understood by us to embrace all changes, more or less, through which the body of a living or extinct organism passes from one epoch, such as the present, into another one, thereby leaving in the strata permanent traces of its characteristic form. We include here a group of observations which are of great importance, but, nevertheless, have been completely neglected by paleontologists.
>
> Fossilization, or rather the process of fossilization, is the kind of phenomenon through which an organized body more or less loses its original, characteristic composition and is converted into a new substance which displays, in the form of an organized body, characters of chemical composition or texture somewhat different from those of the original body. (Translated by W. G. HAKES.)

In 1869, D'ARCHIAC proposed a short and significant definition for fossilization:

> We shall designate under the name "fossilization" the different modifications that the bodies of organisms undergo during their stay in the rocks of the earth. These modifications are frequent, numerous, and highly variable in nature. This has caused many eminent zoologists to make mistakes. Sometimes modifications are so severe that the body's characteristics are completely obliterated. (Translated by CURT TEICHERT.)

The most important aspects of fossilization are biostratinomy and fossil diagenesis. These subjects have been thoroughly discussed by DEECKE (1923), QUENSTEDT (1927), MÜLLER (1951b, 1963), PAVONI (1959), ROLFE and BRETT (1969), and SEILACHER (1973). Some of the possible fates of skeletal material after the death of the organism are shown in Figure 1.

BIOSTRATINOMY

GENERAL DISCUSSION

The term biostratinomy was proposed as "biostratonomy" by WEIGELT (1919)[1] and was originally defined as the study of the manner in which fossils become oriented and arranged in rocks. Today, it has a broader meaning but still embraces the basic concepts developed by WEIGELT. The study of biostratinomy begins with the death struggle of an organism and ends with the final burial and arrangement of the dead or dying animal or its disarticulated remains.

The fate of materials produced and discarded during the life cycles of organisms must also be included in biostratinomy. Examples are the exuviae of crabs, trilobites, and other arthropods, in addition to sporomorphs and fallen leaves. It is important to determine whether an assemblage is autochthonous (*in situ*) or whether it is allochthonous and has undergone postmortem transport and sorting. In both cases, the relative position of assemblages can be entirely or partially altered by internal and

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[1] WOLFF (1954) suggested that the spelling be changed from biostratonomy to biostratinomy in order to make the spelling analogous to stratigraphy. Later, W. KNOCKE (Hamburg) (in VOIGT, 1962, p. 30) pointed out that biostratinomy is the only possible spelling for etymological reasons, but many authors have retained the spelling biostratonomy for reasons of euphony.

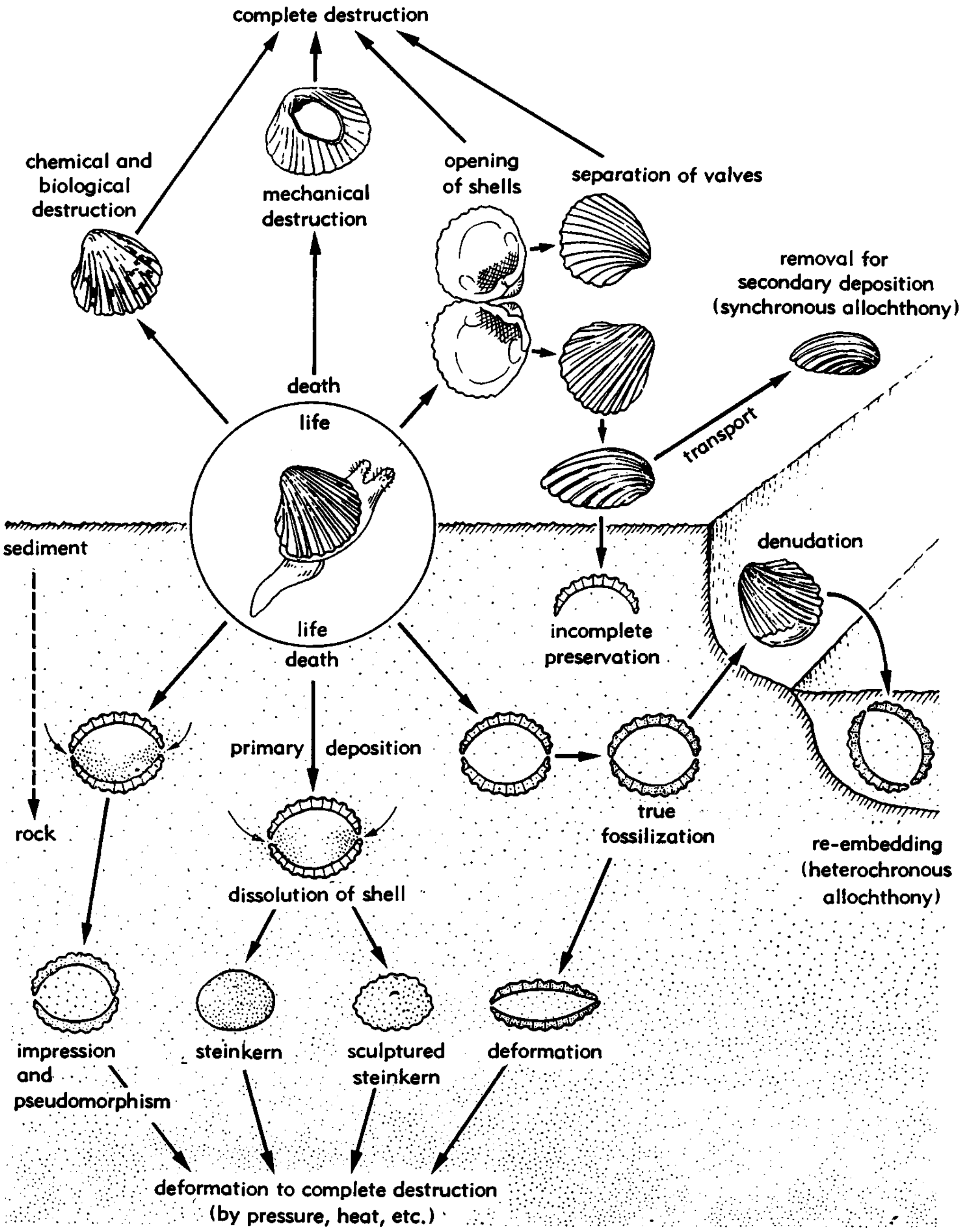


FIG. 1. Diagrammatic representation of fate of skeletal material after the death of the animal (after Thenius, 1963).

external forces such as currents, gravity, buoyancy due to gas entrapment during decay, and predation by scavengers. It follows that the biostratinomer must pay special attention to the original deposit and the types of preservation there. He must also study his material both quantitatively and systematically. Application of the principle of actualism is especially important. Attention must be paid to the recent environment either by direct observation or experimentation, in order to develop a firm base for our knowledge of biostratinomy. In this way, its effectiveness as a tool in the interpretation of ancient environments will be enhanced.

The chance of an organism being preserved as a fossil is dependent upon the conditions of sedimentation, which can, in turn, be related to the paleogeography of an area. Animals living in high altitudes, which are subject to active erosion, are seldom preserved. On the other hand, organisms that live in low-lying areas, or in streams, rivers, swamps, seas, or oceans, stand the best chance of being covered by sediment and eventually being preserved.

The first systematic, biostratinomic observations were made by Walther. Later, the trend for this type of investigation was set by Weigelt, who is considered to be the founder of biostratinomy, and since then, the number of biostratinomic investigations has increased.

At first, incorporation of invertebrates in sediment and the mechanical principles that govern their deposition and arrangement received special attention. Weigelt (1927) has added much to our knowledge of the manner in which vertebrates become buried in sediment, and since the publication of his work on the Kupferschiefer flora (Weigelt, 1928b) interest has also grown in the biostratinomic investigations of fossilized plants.

Biostratinomy originally dealt with idiobiology (namely, the study of organisms as individuals). However, after the work of Wasmund (1926), biostratinomy evolved a biosociologic-biocenologic approach that permitted the interpretation of mode and direction of transport and cause of death in allochthonous fossil assemblages.

The cause of death of a fossilized animal, the manner of its decay, decomposition, and burial in the sediment can be accurately interpreted if its morphology, mode of life, and relationship to the surrounding environment are known. For this reason, it is just as important to have an understanding of ecology and behavior of the animals as to understand geological conditions such as sedimentation. In general, conditions of preservation for aquatic animals are better than those for land dwellers. A similar relationship applies to sessile (attached) or infaunal animals when compared to vagile animals.

The practical importance of biostratinomic knowledge is obvious. In questionable cases, it enables the recognition of *in situ* positions and, by interpretations of current conditions, the original orientation of economic deposits. An outstanding example of this type of investigation was the development of the iron ore deposits of Salzgitter (Germany) by biostratinomic methods (Weigelt, 1923).

In principle, every organic body is preservable, no matter what the proportion of its hard and soft parts. Preservation, in the final analysis, is dependent only upon the dominant physico-chemical and biological conditions to which an organism is subjected. In most cases, the fate of both hard and soft parts is different, and as a rule, the soft parts decompose and decay, leading to a relatively large loss of body material. This process commonly leads to a more or less complete segregation of the more resistant hard parts, which can be broken or macerated depending upon the chemical or physical processes to which they are exposed. It is, therefore, justifiable to discuss the biostratinomy of soft parts and plantlike substances separately from the biostratinomy of hard parts, although transitions between these conditions exist.

Studies of recent processes which especially belong to biostratinomy, are called "actuopaleontology" (Richter, 1929; Dalquist & Mamay, 1963; Schäfer, 1962, 1972).

NECROTIC PROCESSES

DEATH IN GENERAL

In any given case, it is very difficult to determine accurately the exact moment of death, as death is seldom instantaneous. It is almost always linked to a long or short period of progressive deterioration of the metabolic processes, which occurs long before the organism can be considered a cadaver. In higher organisms, cells and cell complexes continue to live for a while after the heart stops beating and, therefore, the end of cardial activity cannot be considered to record the exact moment of death. This is especially true when no external signs of life activity can be observed. In vertebrates, the brain center, which regulates heart activity and breathing, is first affected (Korschelt, 1924). Autolysis leads to an important change in the chemistry of tissues, can influence microbial decay, and is important in the initiation of the partial death and natural rejection of certain body parts. This is especially significant during the molting of arthropods in which up to 90 percent of the covering cuticle is resorbed by enzymatic autolysis (Richards, 1951).

The beginning and end of dying, of course, cannot be determined for fossil material; however, analysis of the manner of burial may lead to useful conclusions about the cause of death, the death struggle, and the death spasms of an animal.

The processes occurring during the death of an organism are called "necrosis." The duration of necrosis varies with the organism and may last for only a few seconds in small organisms, but in large animals may last a considerable time.

CAUSES OF DEATH

GENERAL DISCUSSION

The cause of death is generally quite complex, and in most cases, two or more of the following factors will take part.

External (allogenic) forces. 1) Suffocation—affects all aerobic organisms, if adequate oxygen supply is cut off; 2) starvation—death is caused by prolonged absence of sufficient and properly balanced nutrients; 3) lack of water—death may result from a change in osmotic pressure within an organism; 4) freezing; 5) rise of an animal's temperature above a given level; 6) poisoning through assimilation of toxic, chemically active substances; 7) absence of an adequate light supply, especially important to plants; 8) mechanical vibration, disintegration, and crushing of the entire body or important body parts due to tumbling, lacerating, puncturing, striking, and pinching of important veins; 9) increase or decrease of pressure; 10) infestation by parasites or bacteria.

Internal (autogenic) forces. 1) Old age; 2) organic disease. In this connection it is important to note that for pathological and physiological death, there is no important singular cause.

The number of individuals in a population may be considerably reduced by the regular recurrence of yearly phenomena (dry summer and cold winter periods) or by irregular occurrences (catastrophic climatic fluctuations, disease, volcanic eruptions, floods, severe parasitic activity, and mass appearance of natural enemies). Parasitism and the appearance of natural enemies are commonly the result of a rapid increase in number of individuals within the community that is being attacked. Chetverikov (1905) and Timofeeff-Ressovsky (Timofeeff-Ressovsky, Voroncov, & Jablokov, 1975) referred to such situations as "population waves" *(Populationswellen)*. Mass mortality and the subsequent reduction in population size generally have the effect of increasing evolutionary rates.

DEATH DUE TO OVERGROWTH BY OTHER ORGANISMS

The following are causes of death that are well documented in the fossil record:

Numerous sessile or slightly vagile organisms are able to escape from the danger of overgrowth by organisms of their own or other species by means of various adaptations; however, the animals are often overwhelmed and die. These are mostly animals of flat shape that do not possess the ability to rise coral-like above the sediment. Listed below are examples of free-living, slightly vagile organisms:

1) Massive colonization of oyster banks by *Mytilus edulis*: the meshwork created by the byssal threads of the attached *Mytilus* will entrap enough sediment to suffocate the underlying oyster population and, eventually, the *Mytilus* colonies themselves. These mussel beds then form potential sites for future oyster colonization.

2) *Mytilus edulis* overgrowing *Cardium edule*: living *Cardium* shells are commonly used as sites for colonization by mussels, and it is common to find valves of *Cardium* "spun" together by the byssal threads of *Mytilus edulis*. Death by suffocation therefore results.

3) *Mytilus edulis* overgrowing *Balanus* colonies: *Mytilus* can so completely cover a barnacle colony that the cirri of the barnacles cannot penetrate the byssal threads of

Mytilus. *Balanus*, therefore, dies of starvation (Sewertzoff, 1934).

The mutual overgrowth and encrustation of other animals by sessile organisms has been called immuration by Vyalov (1961). This is a special case in which encrustation occurs only during the life span of the encrusted animal. Encrusting epibionts, in particular, are calcareous algae, poriferans, stromatoporoids, corals, bryozoans, brachiopods, serpulids, bivalves, gastropods, and cirripeds. Following are some examples:

1) Coral covering hippuritids: It is probable that the corals attach themselves to the opercula of the hippuritids at the beginning of their life cycle (Deecke, 1923).

2) Oysters growing on *Balanus*: Barnacles will become completely embedded in the prismatic layer of the bivalves. When the barnacles die and the scutum and tergum pairs fall off, the oyster shells can then begin to fill the hole left by the barnacles in which frequently organic and inorganic bodies, which were either washed in or were in search of shelter, can also be found.

3) When thick shells of oysters or spondylids are sectioned, it is common to find remains of many organisms that have been killed by overgrowth of the bivalve shell. As a rule, such overgrown organisms are well preserved.

It is especially important that this process permits the preservation of organisms consisting of chitin, spongin, plant substance, and so forth, which are not preserved under normal conditions of sedimentation. In this way, the presence of algae, sea grasses, hydrozoans, and ctenostomate bryozoans can be demonstrated (Voigt, 1966; 1968a). Some examples are:

1) Leaf of a sea grass (*?Thalassocharis*) (Fig. 2), serving as a substrate for oysters and showing molds of prodissoconchs of several young oysters, from Upper Cretaceous rocks of the Netherlands.

2) Blades of a sea weed with cheilostome and ctenostome Bryozoa (Fig. 3), serving as substrate for an *Exogyra* from Upper Cretaceous rocks of Belgium. The arrow points to *Stolonicella schindewolfi* Voigt, flanked on both sides by the delicate ribbonlike zoaria of *Taeniocellaria setifera* Voigt. On the lower border of *S. schindewolfi*, transverse structures of the setae are clearly recognizable.

Fig. 2. Leaf of sea grass, *?Thalassocharis*, serving as substrate for oysters and exhibiting molds of prodissoconchs of several young oysters, from Upper Cretaceous (upper Maastrichtian, Tuffkreide), St. Pietersberg near Maastricht, Netherlands, ×6.6 (Voigt, 1966).

3) Immuration and molding of the bryozoan *Onychocella cyclostoma* (Goldfuss) by *Reteporidea cancellata* (Goldfuss) from Upper Cretaceous rocks of the Netherlands. Figure 4 shows the frontal membranes of the closed opesia with the outline of the semicircular operculum.

DEATH FROM SMOTHERING BY SEDIMENT

The chance of burial by sediment is especially great for organisms firmly attached to substrates. Slightly vagile infauna also stand a risk of burial, and are quite commonly embedded in life position; however, such animals are only seldom preserved as fossils because their remains are repeatedly redeposited in shallow-water sediments. Vagile animals are in less danger. Thus, infaunal gastropods are very adept in burrowing upward through thick accumulations of sediment. On the other hand, it has been observed that the starfish, *Asterias rubens*, was unable to penetrate 60 cm of sediment deposited during a storm in less than half an hour (Schäfer, 1962; 1972). This is even more serious when great numbers of these animals are affected and get into each other's way. Their remains are then commonly found with their arms balled up, at an angle to the bedding plane, or overturned. *A. rubens* will often crawl along bedding planes until it becomes stuck and dies. As the sediment impedes forward movement, one or two arms will usually point forward and the rest will drag behind, or else all arms may be directed backward. This type of orientation

FIG. 3. Blade of sea weed with cheilostome and ctenostome Bryozoa serving as substrate for an *Exogyra*, from Upper Cretaceous (upper Maastrichtian, Tuffkreide), Albert-Kanal near Néercanne, Belgium, ×8.2 (Voigt, 1966). Arrow points to *Stolonicella schindewolfi* VOIGT, flanked on both sides by delicate ribbon-like zooaria of *Taeniocellaria setifera* VOIGT. Of particular interest are the transverse structures of the setae, clearly visible near the lower edge.

can occur on the upper surfaces of bedding planes.

Ophiuroids continually work their way upward in the sediment after burial, and in the process become trapped under single bivalve shells, oriented concave side downward. Fossil examples are known from the Upper Muschelkalk of Germany (MÜLLER, 1969a).

Among the Echinoidea, the Irregularia live more or less deeply buried in the sediment, and are in danger of being smothered by it. *Echinocardium* is not able to free itself if it is suddenly buried by 30 or more centimeters of fine sand, which can commonly happen in shallow seas where storms bury numerous individuals at the same time (SCHÄFER, 1962; 1972).

If brachyurans are buried alive and embedded in the sediment, their claws can commonly be found opened slightly and their ambulatory appendages raised above their cephalothorax. This position indicates that the animals raised their legs to lift themselves in the sediment but no longer had the strength to do so (SCHÄFER, 1962; 1972).

DEATH BY OXYGEN DEFICIENCY (ASPHYXIATION)

Aerobic organisms will die if deprived of oxygen. Their needs vary according to degree of activity and environmental conditions. In any given case, oxygen requirements can be extremely different, and such variations are usually determined by the affinity of special hemoglobins for oxygen. The affinity for oxygen in lower animals is many times that in higher ones, whereas conditions are the reverse with regard to carbon dioxide. Humans require an oxygen to carbon dioxide ratio of 250 to 1. In contrast, *Arenicola marina* needs only a ratio of 50 or 70 to 1. Many lower animals, especially polychaetes, can tolerate considerable decreases in the amount of oxygen that they take in without the slightest organic damage. As a rule, such lower animals are endangered only if the oxygen supply is completely cut off.

Many marine polychaetes have the ability to maintain their oxygen requirement by optionally assuming an anoxybiotic existence. The hemoglobin of such animals has an increased affinity for oxygen and the breakdown of stored glycogen enables them to survive in oxygen-deficient environments, in addition to oxygen-rich environments. This is an important fact in the interpretation of ancient environments, as such organisms will succumb only under extremely adverse conditions. This is true for sediments containing FeS_2, if the overlying water is devoid of free oxygen. However, the absence of organic remains does not necessarily mean that a body or layer of water is rich in H_2S (i.e., deficient in oxygen). The absence of the remains of organisms can be linked to other ecological factors such as the lack of suitable nutrients. Environments can be inhospitable only if H_2S is present in the sediment and in the overlying water body. Such types of sediments are most likely to be found in quiet restricted areas with virtually no current activity. In regions where currents do exist, continual poisoning of the water does not occur.

The oxygen content of water is drastically reduced by the decay products of organic material, in particular ammonia and hydrogen sulfide. Reduction in the amount of oxygen is especially severe if there is not a continuous and sufficient supply of fresh water, and if oxygen is not replaced by the activity of plants. If a water body freezes over and the ice is covered with snow, water plants, especially chlorophyll-containing plankton, are able to produce oxygen only if the snow cover is thin. Unless there is influx of oxygen from the outside, the oxygen content is further depleted by decay processes. During winter, many organisms hibernate and thus reduce their oxygen requirements. However, due to the above-mentioned processes, the oxygen content of water is decreased and even can drop below the low level required during hibernation. This will awaken the organisms. Once these animals have awakened, their increased muscular activity increases their oxygen demands in an already oxygen-deficient environment. Because of the ice covering they are unable to reach the surface and the atmosphere, and they perish.

It is well known that mass mortalities of fish, oysters, and crabs occur each year in late summer in Offats Bayou, a narrow marine bay near Galveston Island on the Gulf Coast of North America (Gunter, 1938). The hydrogen sulfide released during decay of the carcasses causes the water of the bay to "boil" over areas as large as 10 m in diameter and to change in color to a turbid red or black. This process begins at the innermost end of the bay and finally spreads into the entire upper part. After a few days, the water becomes clear again, and may or may not remain in this condition for long. Circulation within the bay and water exchange with West Galveston Bay proceed very slowly and cannot be considered extensive, because the mouth of the narrow bayou is extremely shallow. Tides have little effect on the bayou, and denser water settles into the deepest part at the inner end, where it becomes stagnant. It is in these deep areas during the summer months that accumulated organic material decomposes under anaerobic conditions. The gases produced by this process migrate upward through the sediment and enter the upper water layers, causing the death of organisms living there. Presence of hydrogen sulfide plays an important role, as does the anaerobic condition of the upwelling water. In the summer of 1940, the normal mass mortality did not occur, probably because major storms that struck the Texas

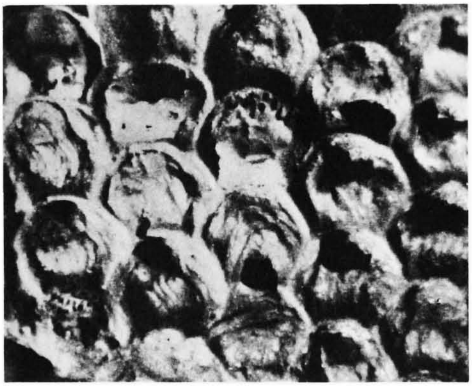


Fig. 4. Immuration and molding of the bryozoan *Onychocella cyclostoma* (Goldfuss) by *Reteporidea cancellata* (Goldfuss) *intra vitam*, with the frontal membranes of the closed opesia reflecting the semicircular operculum. From Upper Cretaceous (upper Maastrichtian), Grube Curfs near Berg in the area around Maastricht, Netherlands, ×16 (Voigt, 1968a).

coast sufficiently aerated the waters of the bayou.

As death approaches in hermit crabs (pagurids), the oxygen-rich currents that circulate through their borrowed snail shells begin to diminish. This reduces the amount of available oxygen in their domiciles and causes the animals to vacate the premises in search of oxygen. Therefore, it is not surprising that the bodies of fossil and recent hermit crabs are invariably found separate from the shells they once inhabited. A similar phenomenon occurs with crustaceans that live in their own burrows or inhabit burrows of other animals. Approaching death weakens the thalassinid shrimp, *Callianassa*, to such an extent that it can no longer maintain adequate currents for oxygen circulation, and therefore leaves its burrow. This helps to explain why crustacean remains are seldom found in supposed fossil *Callianassa* burrows such as *Ophiomorpha* and *Thalassinoides* (Schäfer, 1962; 1972).

DEATH BY SUBMERGENCE OR ENTRAPMENT IN SOFT, INCOHERENT, YIELDING, OR ADHESIVE SUBSTRATES

By observing recent examples, it is known that the death of animals by submergence or entrapment is possible in a variety of natural substances. Although numerous examples have been discovered in the geologic record, only a few are discussed here.

Mud and silt. Muddy substrates can become highly indurated during desiccation; however, their ability to remain firm and to support loads can be quite transitory and can be rapidly lost, as a thorough soaking is usually sufficient to return them to a pliable condition. Animals whose weight exceeds the load capacity of these substrates will sink more or less deeply into the substrate. In many cases, the animals will not remain there and will easily free themselves.

Salt pans and salt-covered muds are widely distributed in the recent environment (i.e., the sabhkas of North Africa, the takyre in Turkestan, and the kewirs of Iran). Within such areas, the exposed parts of partially buried bodies are frequently destroyed by exposure to the atmosphere, removed by scavengers, and eventually transported away by currents. In the Tendaguru beds of East Africa, dinosaur remains are preserved in this manner. Masses of limbs, pelvic bones, and shoulder blades can be found, but only few backbones have been preserved.

Thixotropy plays a large role in these processes; and it is well known that some viscose media can, under mechanical influences, undergo a decrease in viscosity. "Thixotropic consistency" falls somewhere between plasticity and flowability. In such a state, a quasi-solid material that has the potential for flowage exists. The development of thixotropic substrates is dependent upon an increase in the content of clay and water within the sediment.

A potentially thixotropic medium can remain relatively coherent for long periods of time, as it requires a significant change in the physical condition of the sediment to initiate thixotropy. This may be brought about by earth load, and increase in pore water pressure. Especially important is the original water content of the sediment. An animal, beginning to sink in a thixotropic, viscose, muddy medium, will thoroughly agitate that medium in an attempt to free itself. However, this disturbance decreases the viscosity, causing the animal to sink even deeper. Vibration can also play an important part. A stampeding herd of animals can change the physical condition of a thixotropic substrate in which they thereby become entrapped. However, a single animal can easily negotiate such a substrate.

Crude oil, asphalt, and tar. Tar is the hard residue of petroleum with a paraffin base. Asphalt corresponds similarly to the asphaltic oils. Tar and asphalt are both formed when crude oil containing air comes in contact with the atmosphere. Their consistencies can vary from unctuous and soft to hard and weakly brittle. Either in a liquid or later in a more or less soft, solid state, pools of these substances function as traps for unsuspecting animals. Such pools attract animals because of their shiny surfaces, and the smell of hydrogen sulfide attracts scavengers. The struggle of the entrapped animals releases hydrogen sulfide already present in the tar or asphalt, the animals remain stuck, continue to sink, and their bodies attract predators and scavengers. Death by sinking in tar or asphalt is very similar to death caused by sinking into mud, silt, swamps, or quicksand.

Natural upwelling of light paraffin oil is, in general, quite local and inconspicuous, whereas the appearance of the heavy asphaltic oil is more obvious. Light oil is evaporated and easily washed out. The heavier, asphaltic oil appears as dark, tarlike masses, which will undergo a transformation to brittle asphalt. A flowable, dark oil occurs at the center of the asphaltic oil pools, and this is surrounded by a rim of hardening asphalt.

There are numerous examples of pools of asphalt and tar entrapping animals in the recent environment (i.e., Mesopotamia, Syria, Sakhalin, Canada, California, and the Caspian Sea). The best known of these are the asphalt pits of Rancho La Brea in Los Angeles, California. These tar pools have existed since the Pleistocene and are still present, covering an area of 70,000 square meters. The asphalt contained in these pools contains numerous remains of Pleistocene animals (Woodward & Marcus, 1973).

At La Brea, in addition to insects, large numbers of predators (saber-toothed tigers, wolves, leopards, and lynx) and herbivores (deer, horses, camels, elephants, and bison) are found.

The asphalt of McKittrick, California, is another example of an entire fauna such as that preserved at Rancho La Brea.

Occurrences of paraffin seepages are not as well known as those of asphaltic oils. This is primarily because paraffin oils evaporate easily, have a relatively small carbohydrate content, and are easily washed away during precipitation.

Quicksand. Very fine-grained, thixotropic sands are called quicksand. In contrast to other sandy substrates in which animals can become entrapped, quicksand requires a steady upwelling of water. The danger of quicksand and its ability to flow around and engulf an object is directly related to the maintenance of a sufficiently renewable water supply in the deposit. It is the presence of water that decreases grain-to-grain contact. This renders the mass adhesionless and can be easily displaced. The weight of heavy animals will push apart the sand grains, which then flow back over the engulfed animal, and thus trap it.

The most dangerous type of quicksand is formed where water rises from considerable depth under hydrostatic pressure. However, this environment is dangerous mainly to larger animals that have fallen in quicksand. They will thrash about trying to free themselves from the mire and therefore quickly weaken and die. The danger of entrapment of smaller invertebrates in quicksand is less.

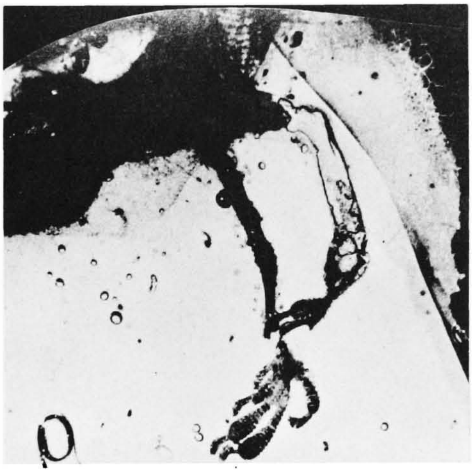


Fig. 5. Part of the head, torso, and forward limbs of *Anolis electrum* Lazell, preserved in resin (Oligocene or Miocene), Chiapas, Mexico; length of forward limbs about 15 mm (Lazell, 1965).

Death in resin. When the bark of a conifer is cut, resin will flow from the wound. This makes it possible to observe recent resin deposits which serve as traps for small flying insects and to compare them with ancient deposits. The best known of these ancient deposits is the Eocene amber of the Baltic region.

Considerable strength is required for an insect caught in amber to free itself Frequently the animal will damage parts of its body (legs, antennae, wings) during the struggle. There is only one known case of a larger animal preserved in amber and that is a small lizard. However, it is quite possible that this lizard was either dead or dying when it was embedded in the deposit. Figure 5 shows the skeleton of the lizard, *Anolis electrum* Lazell, which was discovered in either the Oligocene or Miocene amber of Chiapas, Mexico (Lazell, 1965). The type of preservation and the pronounced broadening at the ends of the toes with a large number of suction cups

FIG. 6. Myriapod, preserved in Eocene amber from the Baltic; length about 5 mm (Müller, 1963).

strongly suggests an arboreal existence for this animal.

If resin has been sufficiently warmed by the sun, it will flow quite easily. Insects embedded in this medium leave little, if any, trace of a death struggle (Fig. 6); however, if the resin is cool (not directly exposed to the sun, possibly in the shadow),

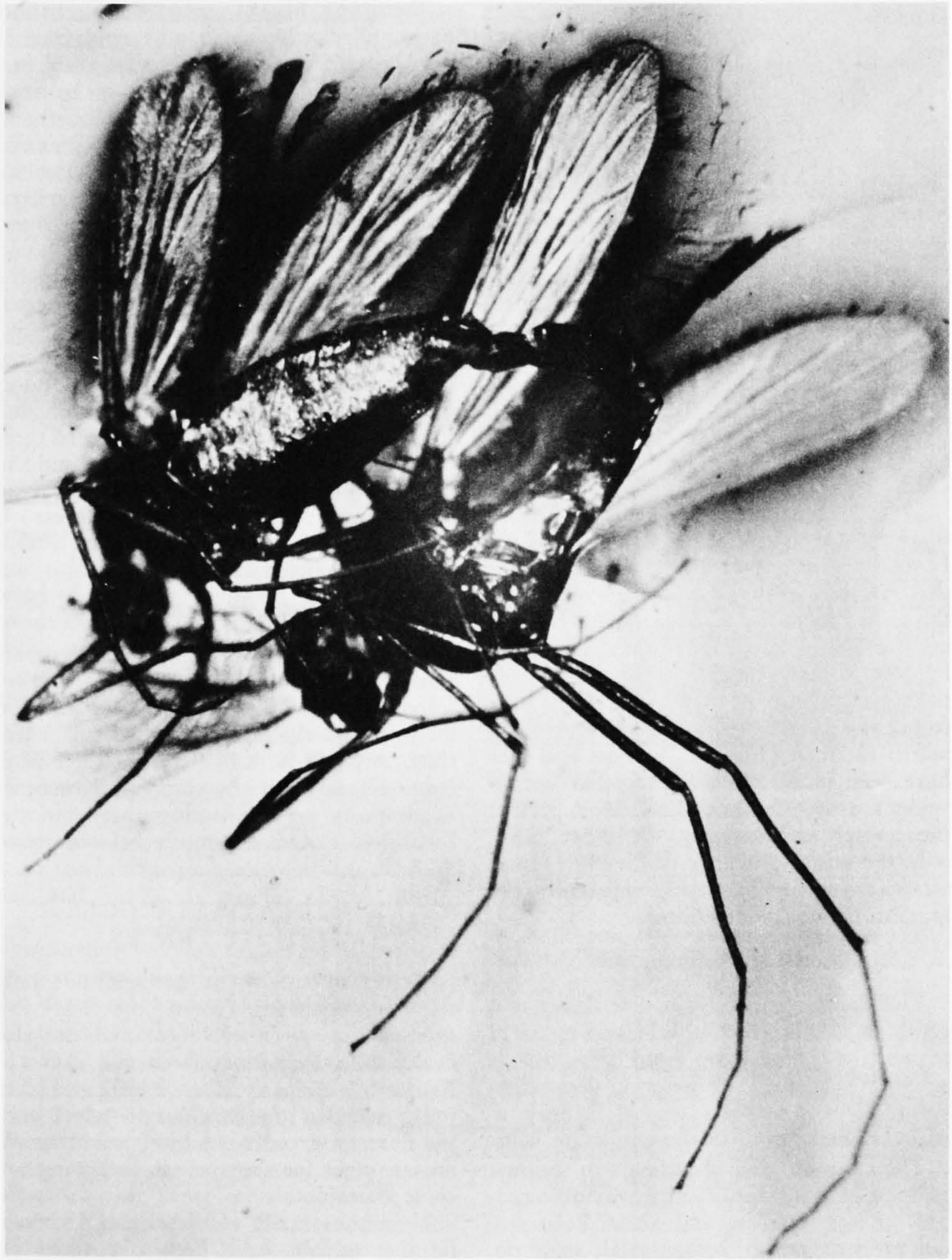


FIG. 7. Flies (Nematocera) in copulation, preserved in Eocene amber from the Baltic (E. Voigt in Müller & Zimmerman, 1962).

it is no longer fluid. Animals entrapped in this type of medium will put up a struggle for varying lengths of time. Examples of rapid embedding have also been observed in amber. Insects engaged in copulation have been embedded so rapidly that they were unable to separate (Fig. 7), and ants have been found with larvae still in their jaws.

When beetles become entrapped in resin,

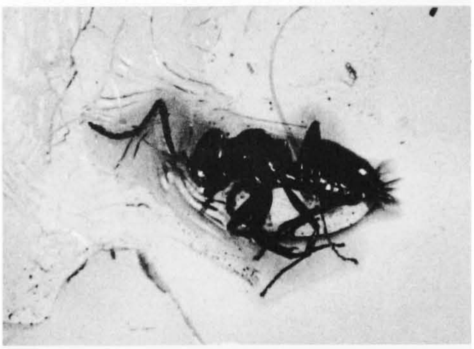


FIG. 8. Ant with its repichnia (locomotion trails), preserved in Eocene amber from the Baltic; length about 2.5 mm (Sektion Geowissenschaften, Bergakademie Freiberg, 249/1; Müller, n).

they violently struggle to free themselves. In many cases, this struggle is so severe that its traces can be found preserved in the amber and the trachea on both sides of the beetle are filled with small air bubbles. These bubbles probably represent the last breath of the animal. Quite frequently ants are embedded during their search for food (Fig. 8). Spiders and flies have been found preserved together with a spider's web. Such finds probably represent the hunter and its prey. In other cases, only the wings and legs of flies are found wrapped in tiny packages, apparently the remains of the spider's dinner.

DEATH BY DESICCATION

The drying up of rivers and lakes is a common phenomenon in arid and semiarid regions. This has also been observed in temperate regions. Wherever desiccation occurs, it often poses mortal danger to many animals, even in the temperate belts.

The concentration of animals in residual puddles of water results in selection according to age, species, and size. Relatively tall animals perish before small ones do, and animals that cannot burrow into the mud die before those that can. Exposed cadavers of vertebrates exhibit positions characteristic of desiccation, with the spinal column flexed dorsally. If firmly held in the sediment, the friable remains of certain organisms (such as the carapace of a crab) will split open upon desiccation.

TRUSHEIM (1938) described a shallow basin, filled with shale and sandstone in the Upper Triassic near Ebrach (Franken). This ancient basin is thought to be analogous to a residual puddle in the recent record. The shale contains many remains of *Triops cancriformis minor* and the undersides of the sandstone beds are covered with a network of delicate ridges, interpreted as the infillings of desiccation cracks that formed in the mud. Therefore, the basin must have been thoroughly desiccated prior to the deposition of each successive bed of sandstone. Each new water current delivered into the basin coarse sandstone, which grades upward into fine sand and, finally, clay. Apparently the death of these organisms was not the result of sudden, catastrophic burial by sand, but was caused by prior desiccation of the mud layers. It is common knowledge that recent *Triops* cannot live out of water.

DEATH BY FLOODING

At the present time, the catastrophic results of sudden floods are well known. Land animals, unless they drown immediately, crowd together on high areas, where they, too, can be killed if the water level continues to rise; however, this manner of death is very difficult to prove in the fossil record and can rarely be interpreted as such.

THE DEATH STRUGGLE AND ITS TRACES

Traces of the death struggle not only tell us something about the last few moments of the life of an animal, but also can yield information about the cause of its death. In many cases, it is possible to judge whether the medium in which animals are preserved was a foreign and hostile environment for the victim. Following are some examples.

Numerous trails of the limulid, *Mesolimulus walchi*, have been discovered on the lower surface of the lithographic limestone of Solnhofen. Usually, the producers of these trails can be found at their terminations. Figure 9 shows such an animal which, during its death struggle, beat its telson several times into the mud.

In the same beds, fossilized cuttlefish (*Trachyteuthis hastiformis* RÜPPEL), have been found, which apparently moved their tentacles across the sediment before dying, leaving numerous impressions. Close to the mouth of the cuttlefish are pieces of another cuttlefish, and it is thought that these fragments may have been the partially digested portions of a cuttlefish regurgitated during the death struggle of the animal.

Many traces of the death struggle of insects are known from amber deposits. If the insects were caught by only their wings or legs, they struggled violently to free themselves and left very characteristic traces. Click beetles (Elateridae) will attempt to free themselves by excited thrashing while other beetles will either spin or swim in circles trying to escape.

RIGOR MORTIS AND ITS TRACES

Shortly after the death of an animal, rigor mortis normally begins, following a period of the death struggle. Rigor mortis spreads slowly, and is typically accompanied by alteration in the position of single parts of cadavers. Thereafter, the effects will gradually diminish. Animals must be rapidly buried after rigor mortis has set in if the rigor mortis position is to be preserved.

In vertebrates, rigor mortis commonly begins eight to ten hours after death and slowly spreads through the body, commencing in the head region, then moving to the neck, and finally the trunk. After about 10 to 20 hours, its effects will vanish and decomposition becomes noticeable. Occasionally, rigor mortis will set in immediately after death of the animal, especially after great physical exertion.

Toward the end of rigor mortis, the clearly visible process of decomposition begins. If the organism is not well buried, decomposition (i.e., muscles) is extensive, and the typical displacement of body parts associated with rigor mortis will not be preserved. In vertebrates, the most common position is a dorsal bend of the spinal column. This shrinkage can be caused by rigor mortis or by a postmortem shortening of the soft parts, or by desiccation. Therefore, the exact cause for the curvature of the spine in vertebrates cannot always be accurately determined.

FIG. 9. *Mesolimulus walchi* (DESMAREST) preserved at end of its trail in Solnhofen Limestone (Malm zeta, lower Portlandian), Solnhofen, Bavaria, approx. ×0.1 (Richter, 1954).

It follows that observations on the death position of animal remains do not allow one to draw conclusions about the life positions of the animals. The death position gives us information only about the moment of death and subsequent alterations of the cadaver.

Glide marks produced by ophiuroids and other well-articulated, lightweight animals can only be made during rigor mortis on suitable substrates. An example of this is in *Geocoma* sp. in the Solnhofen Limestone (Malm Zeta, lower Tithonian) (BARTHEL, 1972).

FATE OF ORGANIC MATERIAL

GENERAL DISCUSSION

Biostratinomic information is not supplied only by the study of hard parts of animals ("true fossils"). There is much to be learned by studying the soft parts of organisms and the products of their decay. After embedding in sediment, cadavers are exposed to interactions with the medium of deposition (air, water, etc.) and the sediment. Variations in these factors, therefore, change the course of the processes of decay and the nature of the end products. If these reactions are known for given conditions, it is possible to draw conclusions concerning different types of fossil soft parts or traces of them.

The process of decomposition of the organic material of plants and animals begins immediately after death. In vertebrates decomposition becomes noticeable only after rigor mortis has ended. The decomposition of soft parts is a chemical process, carried out primarily by bacterial action, and can be divided into two basic groups: 1) aerobic—decay in the presence of ample oxygen, and 2) anaerobic—decay in the absence of oxygen.

Organic material is rapidly destroyed during aerobic decay. The end products of the process are simple chemical compounds that have been extensively resynthesized by microorganisms, leaving only fossilizable body fossils. This process is, therefore, of special geologic interest.

Anaerobic decay occurs under conditions of incomplete reduction in a sealed environment in which concentration of carbon and nitrogen takes place. Even very resistant materials can be metabolized (STEVENSON, 1961). Aerobic decay represents a slow but complete oxidation of body materials. The products of aeorbic decay are, therefore, of less importance than those of anaerobic decay. They consist mostly of simple gases and fluids composed of hydrogen, carbon, nitrogen, sulfur, and phosphorus.

In nature, transitional situations are observed, and aerobic and anaerobic decay is known to occur simultaneously in the same object. Also, after only partial aerobic decay, a body may be transported into a medium of anaerobic conditions, or vice versa. As a rule, however, the process of decomposition is terminated under anaerobic conditions. After embedding, anaerobic decomposition begins. Presence of bacteria and the results of their activity have been demonstrated in many fossils, especially in bones and coprolites.

EFFECTS OF DEGASSING ON ORGANIC MATERIAL COVERED BY SEDIMENT

Gases are produced during the decomposition of organic materials covered by sediment. Under given conditions, these gases rise through the sediment, leaving traces of their movement behind them.

If decay progresses subaqueously, many of these gases are commonly trapped in pockets, such as the abdominal cavities or shells of animals, producing buoyancy. These gases escape into the sediment, and their pathways may be preserved, if the sediment has adequate viscosity and firmness.

Long vertical or inclined cavities in the sediment are called "degassing canals." Their diameters may be several centimeters, but as a rule, lie between 5 and 10 mm. Their lengths can vary and are dependent upon the surface tension of the gas, the thickness of the sediment, the height of water column, and the viscosity and permeability of the sediment. Degassing canals as long as 20 meters have been observed.

In the recent environment, degassing canals are especially well known from sapropelic environments. In sedimentary rocks, it is frequently difficult to recognize degassing canals because they can easily be mistaken for burrows of different types of animals. The same is true for the canals formed in the intertidal zone where air bubbles rise vertically in the sediment. Here, air bubbles are produced when desiccated sand, filled with air, is submerged. On beaches, degassing canals occasionally terminate in small knolls or funnels created by the escaping gas.

If the viscosity and the water and sediment load are greater than the pressure of the gas produced by organic decay, gases remain in the sediment, where they commonly accumulate in rounded or lens-shaped cavities. These cavities can be preserved if conditions of the sediment are suitable, giving rise to vesicular structure. Very large pockets of gases occasionally lead to formation of menisci. Such examples have been found in Walvis Bay in Southwest Africa and in many lakes in northern Germany where entrapped areas of hydrogen sulfide lead to uparching of small islands.

Uparching and collapse phenomena caused by decomposition gases will occur in discrete cavities of sufficient size. In vertebrates the abdominal cavity is commonly filled by gas; in mollusks, the shell.

If gases escape through rupture, or increase in permeability of the walls of the cavity, and if the sediment covering is not sufficiently lithified, collapse can occur. If, however, the cavity is preserved, then it is gradually filled with minerals and becomes a druse. The preciptation of these void-filling cements is commonly initiated in the bottom of the cavity as the trapped gases rise to the top of the dome-shaped structure. Such voids commonly remain open. Frequently large voids, such as those formed by brachiopod shells, are filled with sediment, and a small druse or void can develop near the tops of such shells (Deecke, 1923; Quenstedt, 1927; Teichert, 1930). Thus, geopetal fabrics are produced, which can serve as geologic "bubble levels" (*Wasserwaagen*), making it possible to determine the original horizontal position in disturbed strata and in unoriented hand specimens. Figure 10 shows a cross section through a 3 centimeters-thick terebratulid bed from the Muschelkalk of Gorazde near Gogolin in Silesia. Some of the terebratulids have been preserved in life positions with their beaks pointing downward. The figure also shows that the animals were embedded in the lower part of the bed and then covered with sediment. In each shell, a void filled with drusy calcite is preserved, where decomposition gases accumulated. However, during diagenesis, geopetal fabrics can be displaced to such an extent that it becomes impossible to determine their relationship to the original bedding. Due to dewatering, shrinkage cracks appear in clay and other substances. This is an irreversible reaction in which sediment and parts of shells can be loosened and displaced sideways, even assuming a nested position (Hollmann, 1968a). In such a situation, geopetal fabrics that have formed prior to fossilization may also be used as ancient "bubble levels." This is especially important if the life position of the animal does not coincide with the stable embedding position (Krantz, 1972).

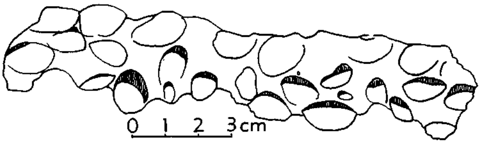


Fig. 10. Cross section through a thin bank of sediment containing *Coenothyris vulgaris* (von Schlotheim), Middle Triassic (Muschelkalk), Gorazde, Poland (Müller, 1951b). The upper portions of many shells have been filled by sparry calcite (lined pattern) which serves as a geologic "bubble level."

These fossil "bubble levels" are also found in coprolites (Fig. 11, 12).

EFFECTS OF DEGASSING ON EXPOSED ORGANIC MATERIAL

If organic substance on the sediment surface or just beneath the sediment surface is exposed to sufficient free oxygen to decompose, all traces of such material will be almost completely lost. After decomposition, the only residuals are simple mineral substances and gases. The decomposition of the animal stops as soon as the remains are covered by a sufficient amount of sediment, and the decomposition products will float and be transported away.

Processes that happen as a consequence of the decomposition of exposed organic material, and the effects of which can still be seen in rock, can also be observed. Decaying organisms, which lie either on the sediment or are lightly covered with sediment, although originally denser than water, rise in the water because of gas produced during decomposition, and become transported pseudoplanktonically. It is necessary, however, that the buoyancy results from the entrapment of gases in a sufficiently large body cavity within the organism.

Special conditions exist as long as soft parts of invertebrates remain in their shells. This commonly occurs with cephalopod shells that sink to the bottom before the body is decomposed (Stürmer, 1967, 1968a,b; Zeiss, 1969; Lehmann, 1967b; Lehmann & Weitschat, 1973). Shells of recent nautiloids containing soft parts are only rarely found. This is probably the result of an early postmortem detachment of the animal's body from the living chamber.

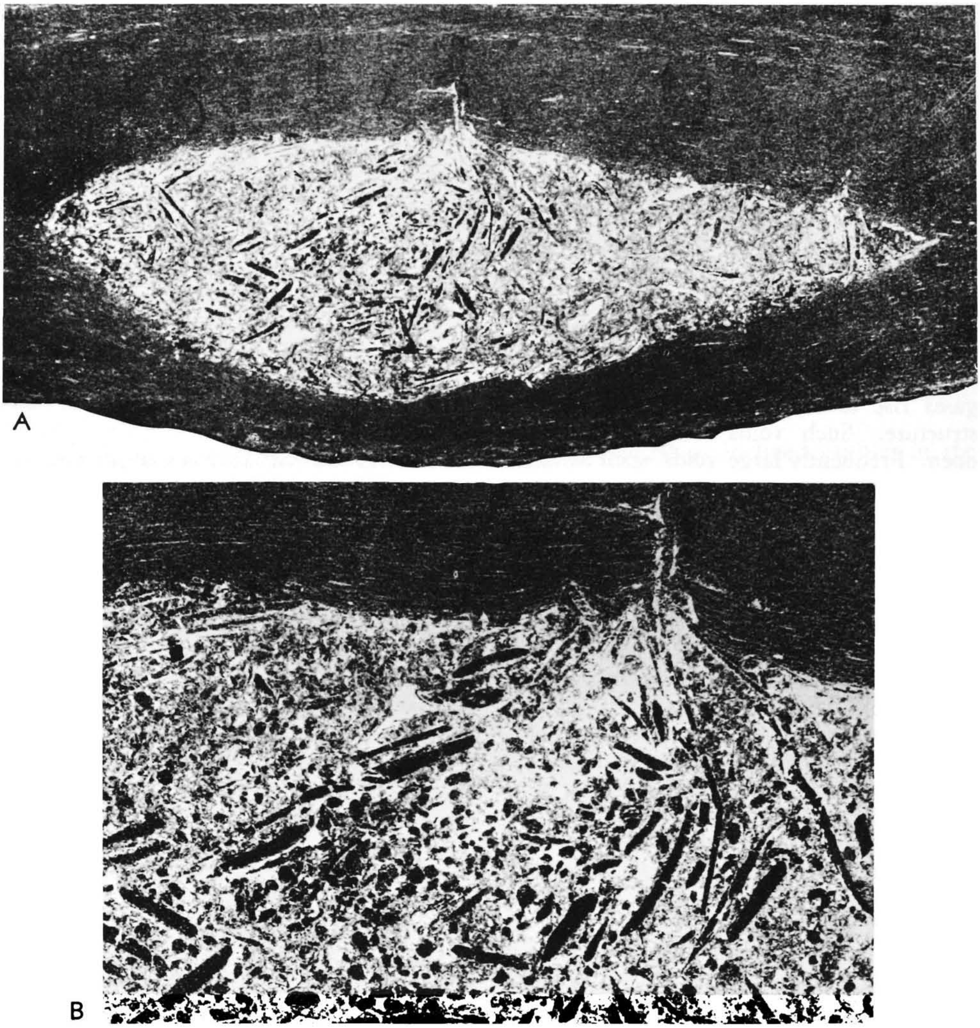


FIG. 11. Cross section through a coprolite (*A*) displaying place of escape for once contained gases produced during decomposition (*B*, enl.), Upper Carboniferous (Staunton, Logan Quarry Shale), Logan Quarry near Bloomington, Illinois. Width of structure is approx. 50 mm (Zangerl, 1971).

The empty shells then drift for long periods of time and are finally cast upon a shore, sometimes in great numbers. The shells of ammonites and nautiloids that leaked and sank to the bottom probably no longer contained soft parts. The shells sank to the bottom in a vertical position and later became inclined as bouyancy diminished. Thus, many perisphinctids in the Solnhofen Limestone are found lying on their sides on bedding planes and have next to them an impression of the venter made when the shells first settled on the sediment (ROTHPLETZ, 1909) (Fig. 13). Ammonites with especially broad venters or long, lateral spines occasionally can be found vertically embedded (Fig. 14). REYMENT (1958) conducted numerous experiments with models of different types of chambered cephalopod shells in order to determine the relationship between the size of the living chamber and the volume of gas contained in the chambers. REYMENT (1970) was able to demonstrate that when

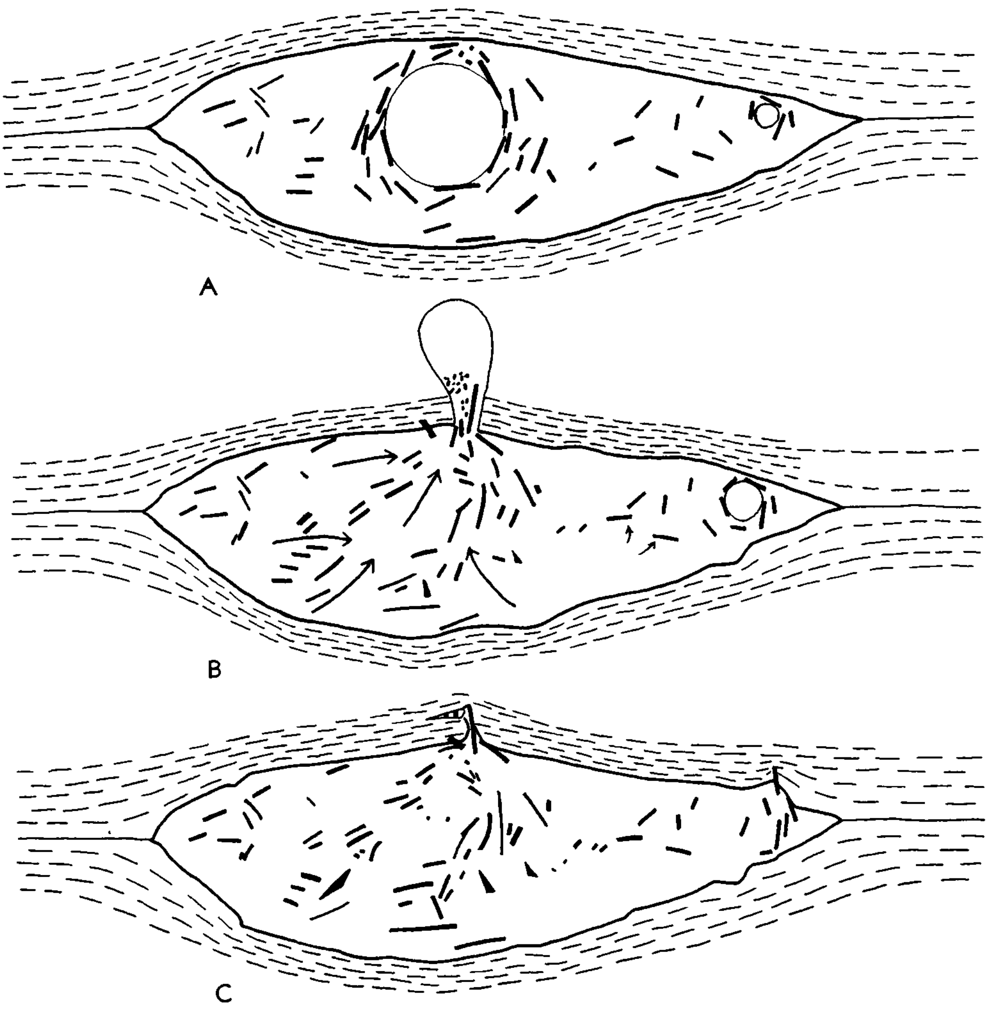


FIG. 12. Schematic explanation for Figure 11.——*A*. During aerobic decomposition, a gas bubble develops.——*B*. The gas bubble escapes from the coprolite through about 2 mm of overlying mud.——*C*. As a result of the rupturing of the coprolite, the fish scales within it are subsequently aligned and compressed. Width of coprolite approx. 45 mm (Zangerl, 1971).

oxycones or cadicones sank to the bottom, they remained in a vertical position for three to four days until the phragmocones filled with water and tipped over on their sides. The closer the shell form approached that of the cadicone, the greater the possibility that the shell would remain vertically embedded in the sediment. Some examples of vertically embedded Ammonoidea and Nautilida can be found in the Paleozoic and Mesozoic rocks of Europe (MÜLLER, 1951b; REYMENT, 1970; VOSSMERBÄUMER, 1972). When ammonoid shells roll along the sea bed, they make distinct skip marks in the sediment, which have been misinterpreted (KOLB, 1961, 1967; SEILACHER, 1963).

Concretionary consolidation during early diagenesis may simulate the effects of buoyancy, if the shell happens to have been covered by a thin sediment layer. This may be observed in many ammonites in the Solnhofen Limestone in which the buildup is several millimeters higher than under the

FIG. 13. Imprint of an ammonite which at first stood in a vertical position on the sediment (top) and then fell over on its side, from Solnhofen Limestone (Malm zeta, lower Portlandian), Solnhofen, Bavaria. Width approx. 190 mm (Rothpletz, 1909).

chambered portion of the shell in which buoyancy existed while the soft parts of the animal remained in the shell during burial (MAYR, 1966).

ROLE OF SCAVENGERS

As a cause of destruction or alteration of soft parts, the role of scavengers is next in importance after the decay of organic material by bacteria. Such animals are: birds of prey (vultures), foxes, wolves, hyenas, many fish (piranha, eels), polychaete worms, snails, crabs, many insects, and insect larvae (ants, maggots). Direct proof of their existence in the fossil record is found only in exceptional cases (mummies; inclusions in resin). In Siberia, cadavers of mammoths partially devoured by wolves and foxes have been found in permafrost. In the ocean, isopods and decapods rapidly destroy dead animals. On land, maggots are particularly effective.

The activity of scavengers and other animals may be estimated indirectly from the amount of coprogenic materials within the sediment. This material influences the composition of the sediment because the amount of excrement produced during the lifetime of an animal is far greater than its body mass. This is especially true for the often very resistant excrement of worms, snails, bivalves, and other invertebrates, which in both fossil and recent deposits may constitute up to 50 percent of the sediment (HÄNTZSCHEL, EL-BAZ, & AMSTUTZ, 1968; SCHÄFER, 1962, 1972).

Some animals that bore into hard parts of other organisms either chemically or mechancially receive their nourishment from the organic material contained in these hard parts (BOEKSCHOTEN, 1966; BROMLEY, 1970; SOGNNAES, 1963), but the physical strength of the bored shells is weakened and their physical destruction accelerated.

SEQUENCE OF DECAY OF SOFT PARTS ASSOCIATED WITH PRESERVABLE HARD PARTS (SELECTIVE DECOMPOSITION)

The skeletal parts of echinoderms are held together only by skin and connective tissue and are easily disarticulated and scattered. If complete specimens are preserved, it is probably because they were buried rapidly and the remains of the animals were resting in an environment free of currents.

Echinoid spines will drop off, seven to ten days after death, due to the progressive decay of soft parts in an aqueous, aerobic environment. If the spines are still attached to the shell, then burial must have occurred while the echinoid was living or soon after death. After 12 days, the apical region of the animal begins to fall apart, starting from the inside outward. After 17 days, only the jaw apparatus and disarticulated elements remain.

The taphonomy of the starfish *Asterias rubens* has been studied by SCHÄFER (1962; 1972) in marine waters of 18°C. After five days the body of the starfish becomes blown up to the bursting point and is easily moved by bottom currents. The integument on the dorsal side of arms and skeleton will then begin to separate from the body, starting at the arm tips. The dorsal integument may then be carried away by currents or it forms folds on the decomposing body. If

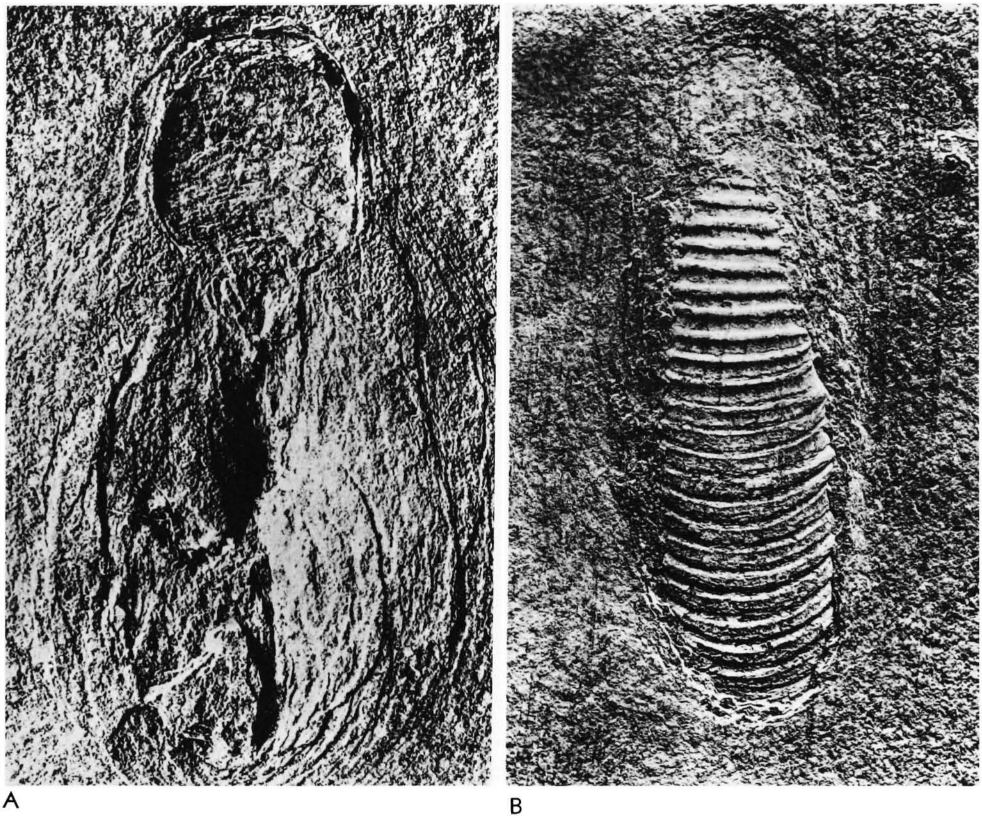


FIG. 14. Vertically embedded ammonite shell; under side *(A)*; upper side of a 12 mm-thick bed *(B)*, Solnhofen Limestone (Malm zeta, lower Portlandian) from Bavaria. Diameter approx. 210 mm (Rothpletz, 1909).

starfish are buried and killed by a thick covering of sediment, the dorsal and ventral skeletons are commonly found wedged together in a tangled heap.

Gas-filled cadavers of holothurians are not buoyant, but are rolled by currents like barrels. Complete decomposition of the thick, hard, resistant dermis may take several weeks. In the absence of currents, the sclerites are deposited in small clusters in the sediment.

SCHÄFER (1962, 1972) has demonstrated that recent coleoids become buoyant immediately after death and will remain afloat at the surface for many days, depending upon the water temperature. The body of the animal is almost totally decomposed before parts of it begin to fall to the bottom. This explains why the soft parts of coleoids are rarely preserved even in fine-grained sediment under anaerobic conditions generally favorable for the preservation of soft parts. Soft parts or the impressions of coleoid soft parts are almost always found in nearshore sediments which were periodically dried out. Only during these periods of exposure are the animals dense enough to sink into the sediment, and then be completely buried by sediment (ABEL, 1916; NAEF, 1922; JELETZKY, 1966).

The drifting coleoids quickly lose their very porous, mostly calcareous cuttlebone, which can float for considerable distances and can serve as a site for attachment of many kinds of organisms. The cuttlebone is commonly destroyed by the action of boring algae or by the pecking of sea birds. Larger fragments rarely stay afloat for more than eight days. In contrast to shells of *Nautilus* and of ammonites, the cuttlebones of sepiids do not settle to the bottom of the sea, but may accumulate in large numbers along beaches. The prominent, mostly chitinous cuttlebones of the Teuthoidea are not buoyant and sink immediately to the bottom where they are embedded together in areas with entire bodies of the organisms, unless strong currents are present. The ink sac is very durable and is occasionally found inside the animal (ABEL, 1916; NAEF, 1922; EHRENBERG, 1942; JELETZKY, 1966; STÜRMER, 1965, fig. 5).

FATE OF PRESERVABLE HARD PARTS BEFORE FINAL BURIAL

GENERAL DISCUSSION

Accumulations of hard parts of animals become sedimentary constituents and therefore obey the laws of sedimentation. Therefore, it is possible to draw many conclusions about the type of sedimentation by studying the interrelationships of the preservable parts of organisms. It is also necessary to study the relationship of hard parts to the surrounding rocks before and during the embedding, as well as the mechanical and chemical changes of the hard parts induced by biologic and inorganic factors.

Accumulations of fossils are burial assemblages or thanatocoenoses (WASMUND, 1926). There are basically three types of thanatocoenoses: 1) autochthonous—life assemblages; 2) allochthonous—assemblages that have been transported over varying distances; 3) assemblages of living organisms that have been washed into hostile environments where they died.

The composition of a thanatocoenosis is strongly determined by the nature of the constituents of the biocoenosis. In **autochthonous thanatocoenoses**, the composition of life and death assemblages are identical, and they reflect the conditions of the biocoenosis. They allow certain conclusions as to the factors that influenced the biocoenosis such as conditions of feeding, respiration, and adaptation. Autochthonous thanatocoenoses are limited in space and dependent on the ecologic conditions of the environment, and must be understood as parts of ancient biocoenoses. Associations of trace fossils (ichnocoenoses, proposed by DAVITASHVILI, 1945) can be considered as biocoenoses as well as thanatocoenoses because, as a rule, they are autochthonous.

TABLE 1. *Different Types of Fossil Accumulations (Fossil-Lagerstätten) (modified from Seilacher, 1970; Reineck & Singh, 1973).*

1. Enriched deposits (*Konzentrat-Lagerstätten*). Concentrated accumulations of disarticulated skeletal material.
   a. Condensation deposits. Concentration of skeletal material due to slow rates or the absence of sedimentation. Examples: submarine cave deposits, condensation horizons.
   b. Placer deposits. Concentration of hard parts due to transport and sedimentary sorting. Examples: Bone beds, allochthonous amber deposits.
   c. Sedimentation traps. Inorganic filling of cavities. Examples: terrestrial and submarine fissure fillings, burrow fillings.
2. Conservation accumulations (*Konservat-Lagerstätten*). Characterized by the complete or partial preservation of soft parts and the common preservation of complete, articulated skeletons.
   a. Stagnation deposits. Accumulation of organic remains in sapropelic sediments where water layer directly above sediment surface is anoxic. Examples: black shales, lithographic limestones.
   b. Conservation traps. Rapid sinking and embedding of organic remains into preservational medium or cavities. Examples: amber, peat, asphalt.
   c. Burial deposits. Rapid embedment of organic remains in reducing sediments. Examples: Hunsrückschiefer, Sendenhorst fish deposits.

Allochthonous thanatocoenoses (taphocoenoses, QUENSTEDT, 1927) are formed by the transport of material and the processes of demixing, sorting, and destruction that occur during transport. These processes also act upon the inorganic, clastic constituents of the surrounding sediment. Thus, the resistivity of skeletal material against attack by chemical and physical forces prior to burial is of utmost importance. The composition of a thanatocoenosis can be drastically changed by the elimination of certain forms, and the individuals found in thanatocoenoses are commonly those elements of the biocoenoses that were most resistant to selective abrasion and diagenesis. In many cases, thanatocoenoses contain autochthonous as well as allochthonous elements. Accumulations of products of special life cycles such as exuviae, leaves, and sporomorphs have been called **pseudocoenoses** (MARTINSSON, 1955).

Naturally, the degree of transportation can be subject to important change, and many different types of sorting can result. On the other hand, tectonic or astro-climatic cycles and rhythms can create repetitive sequences of conditions of burial. The fact that 44 percent of the animals in the animal kingdom lack hard parts explains incompleteness of the fossil record as well as the fact that fossil plants are much rarer than fossil animals.

SEILACHER (1970) proposed a classification of fossil deposits which he called "*Fossil-Lagerstätten*." These deposits are arranged according to their mode of formation and the general shape of accumulation (Table 1).

ALLOCHTHONOUS BURIAL

GENERAL DISCUSSION

Transportation causes mechanical destruction of organic material as well as segregation of particles according to shape, hardness, and weight. Small bioclastic particles, just as other sedimentary materials, may be redeposited several times. There is a direct relationship between quality of preservation and time of transport. However, particles may even be further destroyed *in situ* by abrasion in turbulent water. In general, the destiny of hard parts is dependent upon the relationships between the rate of deposition and reworking.

SORTING BY TRANSPORTATION

This process can be defined as the sorting and deposition that results from differences in form, hardness, weight, and durability of shell material and the related chemical and mechanical processes. It can be simulated by the following processes: 1) biological causes, 2) selective removal of certain ontogenetic stages through death, and 3) diagenetic processes after embedding.

Diagenetic processes can wholly or partially (often selectively) destroy, or render unrecognizable, the fossil contents of a rock.

Selection by death occasionally plays a large role. Thus, WASMUND (1926) observed how in early spring, numerous, immature specimens of *Limnaea stagnalis* and *Limnaea auricularis* daily formed allochthonous thanatocoenoses along the shore of Lake Constance. Accumulations of adult shells were rare. In general, only single shells were washed ashore.

The reason for these accumulations is related to the climatic conditions of early spring. During warm days, the animals move upward *en masse* in the sediment and appear at the surface, where they are killed by frost during the following night. WASMUND (1926) also reported observation of a *Spülsaum* of dead larvae of ephemeral flies in a sand bar of the delta of the Rhine on the Austrian shore of Lake Constance. Larvae crawled onto south-facing cliffs, thus escaping from the cool water into the sun and warm breezes. They were then killed by night frosts and added to the enlarging *Spülsaum*. Both of these allochthonous thanatocoenoses were thus caused by local meteorologic catastrophes.

The shells of gastropods are commonly removed by hermit crabs (Paguridae) (SCHÄFER, 1955). Hermit crabs prefer particular shells, and this simulates selective sorting by transportation. Accumulations of only large cutting and crushing teeth of skates and sharks are another example. These animals shed their teeth in the same area for many years. The growth and eventual loss of teeth is related to the reproductive process and change of teeth usually occurs during mating, which commonly takes place in the same area, year after year (SCHÄFER, 1962; 1972). The smaller grasping and crushing teeth fall out all year long and are found widely scattered over the sea floor. Mechanical sorting can also be simulated if organisms of the same age and size settle and colonize a particular substrate.

Marine invertebrates, such as clams, snails, and crabs can be transported by other animals to the land and become embedded in lacustrine or terrestrial sediments far from the sea. This, for instance, is done by the sea gull *Larus argentatus* which feeds mainly on clams and snails, but also on crabs and fishes. During the mating season such prey is offered ceremoniously by males to females. These, and indigestible, regurgitated remains, pile up in the nesting territories and represent a special case of autochthonous sedimentation. Small clams which have been swallowed whole and regurgitated are of an even size and such accumulations can be mistaken for results of current sorting (TEICHERT & SERVENTY, 1947; GOETHE, 1958).

Wind occasionally plays an important role in the transportation and sorting of organic remains. This is especially true for small bones in which the periosteum and marrow have disappeared. The periosteum and marrow together can account for up to two-thirds of the total weight loss of the bone. The pneumatic bones of birds are especially light. A humerus of the crow, *Corvus frugilegus*, which was 5.4 cm long, weighed only 1.32 gm. On salt-encrusted sand flats of the island Alte Mellum near Wilhelmshaven, vertebrae of seals have been seen to be moved by wind at velocities at which small valves of *Macoma* and *Mactra* as well as the rounded shells of *Littorina* were not moved.

It is necessary to be especially careful in the study of separation of clam shells, the right and left valves of which are often deposited in different places. This is easily explained if form and weight of the two valves differ much, as, e.g., those of *Gervillia (Hoernesia) socialis* of the Upper Muschelkalk. Even in equivalve clams, differences in form and weight of the valves exist. In equivalve heterodonts and schizodonts, the right valve is generally heavier because it carries large hinge teeth. These examples demonstrate that it is necessary to exercise caution in the evaluation of fossil concentrations, especially those consisting of individuals or fragments of equal sizes. In such cases it is necessary to have independent evidence of mechanical sorting by currents. In *Cardium edule*, the weight difference between right and left valves ranges from 0.72 to 4.38 percent (KLÄHN, 1932). The specific weight even in different valves of the same species varies so much that it must be considered when studying the sorting process affecting bivalve shells.

The significance of these factors related to the sorting of bivalves is enhanced by the hinge teeth and chondrophores acting as anchors. The right valves of desmodonts do not possess a chondrophore and therefore are more easily transported than the left valves which have chondrophores and, therefore, offer more resistance to movement. If a large colony of mussels (*Mya arenaria*) is churned up by waves, the chondrophore-bearing left valves are transported lesser distances than the right valves which lack chondrophores. Large accumulations of these shells can form belts 10 to 50 m wide consisting of up to 90 percent of one valve and 10 percent of the other. An admixture of different types of valves usually results from the addition of new shell material from another nearby colony. In tidal channels, it is quite common to find valves without chondrophores transported over long distances (RICHTER, 1922).

Durability strongly influences the preservation of shell material in the face of mechanical processes, both within and on the sediment. Some shell parts may be completely destroyed as, for example, in some bivalves of which only one valve remained for a long time. Such valves may even now be rarities (e.g., the right valve of the pelecypod, *Eopecten albertii*, found in the Muschelkalk in the Germanic basin). Small shell components are more easily destroyed than large ones (HALLAM, 1967).

The presence of worn-down, delicate, or easily fragmented hard parts, which have most probably been redeposited together with the surrounding sediment, may make it possible to draw conclusions about the length of transport. Only very durable skeletal material can survive long transportation in coarse-grained sediment. Mechanical abrasion and faceting will quickly destroy any fragments having little durability. Thin and friable bones of animals found in Pleistocene caves are examples of skeletal material that has not been transported great distances. Observations of redepositing have shown that such occurrences are geographically local and are accomplished during short periods of inundation. This is especially true for fragile, allochthonous remains of recent mollusks.

As a rule, animals living on the sediment stand a better chance of being redeposited than those living within the sediment; however, destruction is not necessarily the same for all hard parts because infaunal organisms tend to have less durable shells than do members of the epifauna.

Table 2. *Floatability Constants for some of the Most Common North Sea Bivalves (after Tauber, 1942).*

Number of Specimens Studied	Species	Average Surface Area (mm^2)	Average Weight (gm)	Floatability Constant
12	*Cardium edule*	1,930	2.85	169
8	*Mya arenaria*	7,258	7.10	255
15	*Mytilus edulis*	1,962	1.30	377
20	*Macoma baltica*	330	0.27	305

MECHANICAL DESTRUCTION OF HARD PARTS PRIOR TO BURIAL

Hard parts of organisms may be destroyed by biologic or by entirely inorganic processes. Biologic processes as well as inorganic, chemical processes are discussed at length elsewhere.

The degree of physical destruction of shell material allows one to draw conclusions as to the mechanical processes in operation during the period of shell destruction. This is especially true for conditions of sedimentation. Therefore, it is not only necessary to know what kind of destruction occurred but also the speed at which it took place. These mechanical processes can be divided into two basic types: 1) polishing or abrasion, and 2) breakage or crushing. Because of their abundance and availability, the hard parts of mollusks have received considerable attention in the literature with respect to these destructive processes. Therefore, they are discussed in detail below.

Ambient polishing. If one considers the appearance of the destroyed shell material and the composition of the allochthonous thanatocoenosis, the diversity in preservation is conspicuous (e.g., in shell accumulations along swash marks *(Spülsaum)* or along sandbars). The following are causes responsible for this condition: 1) different resistivity of the shells against chemical, mechanical, and biological destruction (Chave, 1964), 2) differences in the ability to float, and 3) different behavior on the sedimentary surface (i.e., rolling, gliding, etc.).

A basis for estimating floatability was developed by Tauber (1942) who divided the surface area of the shell (in mm^2) by the four-fold value of its weight in grams. The area is determined by rolling the shell along millimeter graph paper and counting the number of covered millimeter squares. Table 2 shows the floatability constants of some common clams found along the North Sea.

Because of their greater floatability, shells of *Mytilus edulis* and *Macoma baltica* are more easily moved by transporting media than those of either *Cardium edule* or *Mya arenaria*. Therefore, shells of the two last-mentioned species, as a rule, move with the sand inside a sand bank whereas *Mytilus edulis* and *Macoma baltica* are commonly transported across the sand in the turbulent zone of shells (Klähn, 1932). This explains the observation by Klähn (1932) that shells of *Cardium* and *Mya* are commonly strongly polished, whereas those of *Mytilus* and *Macoma* rarely are polished at all.

Differences in floatability of shells is a result of the relative resistivity of different bodies. This is the reason for differences in degree and type of mechanical, and, to some extent, biological destruction of shells.

If biological factors are ignored, the mechanical destruction of shell material in coarse-grained sediment (gravel) results generally in total destruction of the shells, whereas in finer grained, sandy sediment (especially for grain sizes between 0.5 and 0.005 mm), polishing takes place. In addition to sand, shell debris also acts as a polishing agent, whereas the mechancial effect of the silt and clay fraction on shell material is minimal.

Ambient polishing can result from 1) mass transportation in churned-up sand bodies, and 2) rolling of shells over an abrading sediment surface. Mass transport in the marine environment is characteristic for sand banks and giant ripples. The second method of polishing occurs mainly in the surf zone, but also in the terrestrial environment, especially in dune and desert areas.

During polishing of bivalve and gastropod shells, the periostracum and the fine details of the shell surface are destroyed. In bivalves the ornamentation and hinge teeth are also lost, and the edge of the shell is rounded. The valves of bivalved shells exposed to ambient polish soon become separated. In addition to being destroyed by organic decay, the ligaments are gradually loosened, and torn or filed through.

KLÄHN (1932, 1936) has made quantitative investigations on the type, manner, and duration of reworking, and mechanical destruction of mollusk shells. In general, the percentage of reworked shells is less for small forms than for large ones (see also HALLAM, 1967). The relationship is just the opposite of that for the chemical dissolution, which is inversely proportional to size of shell materials. The reason for this phenomenon is clear. Smaller forms have a relatively high floatability and sink slowly. The more bulky the shell, the greater the tendency for it to remain near the sea bottom where polishing occurs. However, correlation between the degree of polish and the initial weight of the shell may also be negative. This is especially true when there is a disproportionate increase in shell thickness with increasing length. Also, angular sand grains are more effective polishers than rounded ones, and fine grains more effective polishers than coarse grains, because they move more swiftly with the water. Single valves are more rapidly polished than closely packed accumulations of shells that protect each other from destruction. Experiments performed on the tumbling of pea-sized shell material show that more abrasion occurs within the first nine hours of tumbling than later (HALLAM, 1967). The sculpture on the convex side of the shell is usually the first to be worn away, and this usually occurs within the first nine hours of rolling. On the other hand, structures of the protected, concave surfaces of shells are commonly preserved for long periods of time. Dense, fine-grained skeletal parts are more resistant than porous ones, and rounded parts more than flat bodies (e.g., snail and bivalve shells).

Faceting. In addition to, or in place of ambient polish, shells may be polished on only one side. This process is called faceting, and the shape and position of the facets is determined by the abrading medium and by the properties of the abraded body. Commonly, faceted objects appear broken. MÜLLER (1951b) distinguished three types of facets: anchor-facets, roll-facets, and glide-facets.

1) Anchor-facets. Anchor-faceting (or sand-polishing in the sense of PAPP, 1941) occurs when hard parts of organisms are firmly anchored in and project slightly above the surface of the substrate. If abrasive materials move across them, they are faceted. This process is similar to glacial erosion. Faceting of this sort differs from roll-faceting and glide-faceting in that the shell material is firmly embedded in the substrate.

A unidirectional current produces a single, oriented facet. If currents are changeable or the object shifts its position, many different facets may be produced on the same object. In addition, anchor-faceting can be produced on the opposite side of the anchored object, if this has been flipped over by currents. The resulting facet will lie more or less parallel to the first facet. If an object has been shifted several times, it may become firmly wedged between pebbles, and different sides may then be faceted, and the facets need not necessarily be parallel. One object may have anchor-, roll-, and glide-facets.

As carrying media for the abrasive material, water, air, and ice are of primary importance; coarse-grained sand is the most important abrasive. Because coarse-grained materials are commonly transported only in shallow water, anchor-faceting is especially characteristic of beach and nearshore deposits. On land, this type of faceting occurs in dune areas, as described by PAPP (1941) for shells of *Pisidium* and *Dreissena* that had been transported by the wind.

Because faceting can take place only in a flowing medium, shells are oriented in their most stable position. Faceting then affects the upper side of the shell. Dish-shaped bodies (single valves of mollusks, patellids, etc.) are turned on their valve margins; high-spired gastropods are mostly turned on their apertures, and cone-shaped bodies (e.g., shells of *Trochus*), whose basal diameter is equal to or greater than their height come to rest on their base. In such spiral forms, the tips of the cones are polished first. The position of facets is, therefore, dependent upon the shape and statics of the body being polished.

With progressive polishing or sandblasting, bowl-shaped objects (such as single valves of bivalves and patellids) assume a ring-shaped appearance. The resulting rings are very fragile and easily break up into shell debris. Fossil examples have been described by PRATJE (1929) from the upper Pliocene (Red Crag) of Foxhall near Ipswich, England, and also from the Vienna Basin. Such occurrences can be documented if shells are preserved, especially in younger strata. Otherwise, they may be mistaken for accumulations of debris caused by accumulation of decomposition gases in the arches of the shells.

2) Roll-facets. Another type of faceting can develop by the continual shaking of bivalve shells with sand, as has been demonstrated experimentally by KLÄHN (1932).

Where roll-faceting occurs in nature, it is found under conditions that correspond to the above-mentioned experiment. These are: 1) relatively coarse-grained sand substrates, 2) relatively strong turbidity, especially in nearshore environments, and 3) especially strong, fluctuating rates of movement that persistently cause rolling and tumbling (i.e., tides, strong longshore currents).

Roll-faceting acts especially on bivalve shells, but it is also common in shells of snails and other hard-shelled animals. Generally, in rolled bivalve shells abrasion begins at the umbo. PRATJE (1929) called this type of abrasion "umbo-faceting." Similar abrasions may be found in the middle of the valves of bivalves such as *Scrobicularia plana* and *Mactra corallina cinerea*. HOLLMANN (1968c) called these "median-facets." Shells abraded in this manner first take on a rounded appearance and then the abraded area progresses from the hinge out following growth lines. Eventually the shell takes on a horseshoe-shaped appearance. On this basis, one may distinguish between roll-faceting, round hole-faceting, and horseshoe-faceting (TAUBER, 1942).

The conditions for the formation of roll-facets are present mostly on sandy beaches in the intertidal zone. In this area, faceting of this type is so common that the term "tidal-faceting" has been proposed and, if observed in ancient sediments, presence of tidal flat conditions may be deduced (KÜPPER, 1933); however, because such forms are also observed elsewhere, under conditions of strong movement and an abrasion substrate, the term "roll-facets" seems more appropriate. Roll-faceting is also known from tideless coasts or coasts where tides are weak, such as the Baltic, Adriatic, and Black Seas. In these regions, abrasion is caused by fluctuating coastal currents. As might be expected, the occurrence of roll-faceting is much less frequent than in areas of stronger tidal currents. PRATJE (1929) cited fossil examples from the English Red Crag and noted that they appeared absent in the Mediterranean Vienna Basin. PAPP (1941) studied abraded parts of *Dreissena* and *Pisidium* and observed that holes were worn in the umbal area of the shell. He deduced that such faceting was the result of movement of the shells over the sands of wandering dunes. Thus, roll-faceting has been shown to occur in marine to continental conditions.

The position of the facet in relation to the shell margin depends on the roundness of the shell. In bivalves, the angle between the facets and the shell margin is generally large. In *Cardium edule* it varies between 30 to 90 degrees. KLÄHN (1932) performed an experiment to study roll-faceting, using the following materials: 10 cm^3 of sand with a grain size between 0.25 and 0.12 mm, 100 cm^3 of water, and *Cardium* shells 1.8 to 2.4 cm in length. This mixture was then tumbled for 92 hours, at 106 revolutions per minute, in a tumbling machine. The first effect on the shells was the development of a small hole in the umbonal region, which gradually increased in size as did the angle of the facet in relation to the shell margin. After 160 hours of tumbling, the angle had increased to 50 degrees. The process took much longer for smaller shells.

3) Glide-facets. Glide-faceting results when hard parts of animals glide over abrasive substrates such as coarse-grained

sand. As in anchor-faceting, a flow medium must be present for glide-faceting to occur; however, glide-faceting results when shells are not anchored in the substrate. Under these conditions, cone-shaped shells, with basal diameter greater than height, glide along on the larger apertural end, which is worn away. In some cases, faceting is so severe than only the points of the shells remain. This is characteristically observed on shells of *Trochus* and similarly shaped shells in which glide-faceting was first reported.

A special case of glide-facets is produced by pagurids. Most hermit crabs inhabit the littoral zone where in places they are so abundant that they occupy practically all empty gastropod shells. The crabs are generally quite active and drag the shells they inhabit along the ground so that they become faceted, especially on sandy substrates (pagurid-faceting). Most severely affected are usually the parts near the aperture, in dextrally coiled shells the left outer side of the last whorl. This characteristic position makes it possible to demonstrate fossil occurrences of pagurids, even if the crabs themselves are not preserved.

Table 3 shows the different types of faceting observed on short-conical gastropod shells.

Table 3. *Faceting Present in Short-conical Gastropod Shells.*

a) Glide-faceting
Parallel to the base on the apertural side

b) Anchor-faceting
Parallel to the base on the pointed side

c) Pagurid-faceting
Somewhat to the side of the oldest whorl on the apertural side of the shell and somewhat higher on the shell than the initial glide-facet

FRACTURING

If biologic factors are excluded, mechanical fracturing of shells occurs mostly through the interaction of shells with coarse-grained sedimentary particles over which the shells are shoved, skipped, and rolled. In flowing water, mechanical fracturing occurs in river beds and along pebbly or gravelly shorelines of the sea. The action of the waves alone may have similar effects. Complete destruction of organic debris generally does not occur below effective wave base at 50 to 60 m. Tidal and "exchange" currents, which occur at greater depths, do not have sufficient strength to fracture shells, such as those of mollusks.

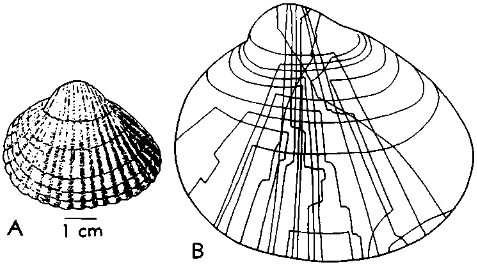


Fig. 15. Fracture deformation of recent *Cardium edule* Linné (*A, B*) collected from broken shell masses along the shore, Scheveningen and Kattwijk, Netherlands (Hollmann, 1968b).

When the fragments of shells have not been completely separated, their arrangement can sometimes simulate the impression in the sediment of artificially crushed shells.

Klähn (1932) demonstrated quantitatively that if bivalve shells are shaken together with pebbles, abrasion plays only a subordinate role in the destruction of the shells. Because of the relatively large size of the pebbles more uniform surfaces are present that can strike against and therefore break the shell material. On the other hand, if bivalve shells are initially tumbled in sand or a similar medium, the dominant process of abrasion will give way to breakage. As the shells become increasingly thinner due to the polishing process, they become more easily fractured. Cracks appear and eventually they fall apart, and the pieces are deposited as accumulations of shell fragments.

Mollusk shells are mostly fractured by hard impacts. The broken edges are, as a rule, very irregular and follow structurally weak parts of the shell. Determining factors are their laminated structure, differences in thickness and convexity, relative size, ornamentation, and microstructure (Kessel, 1938; Schäfer, 1962; 1972; Hollmann, 1968b). The nature of primary accumulations of shell debris is determined by the mechancial resistivity of the shells and varies from species to species.

Bivalve valves with well-developed, radial

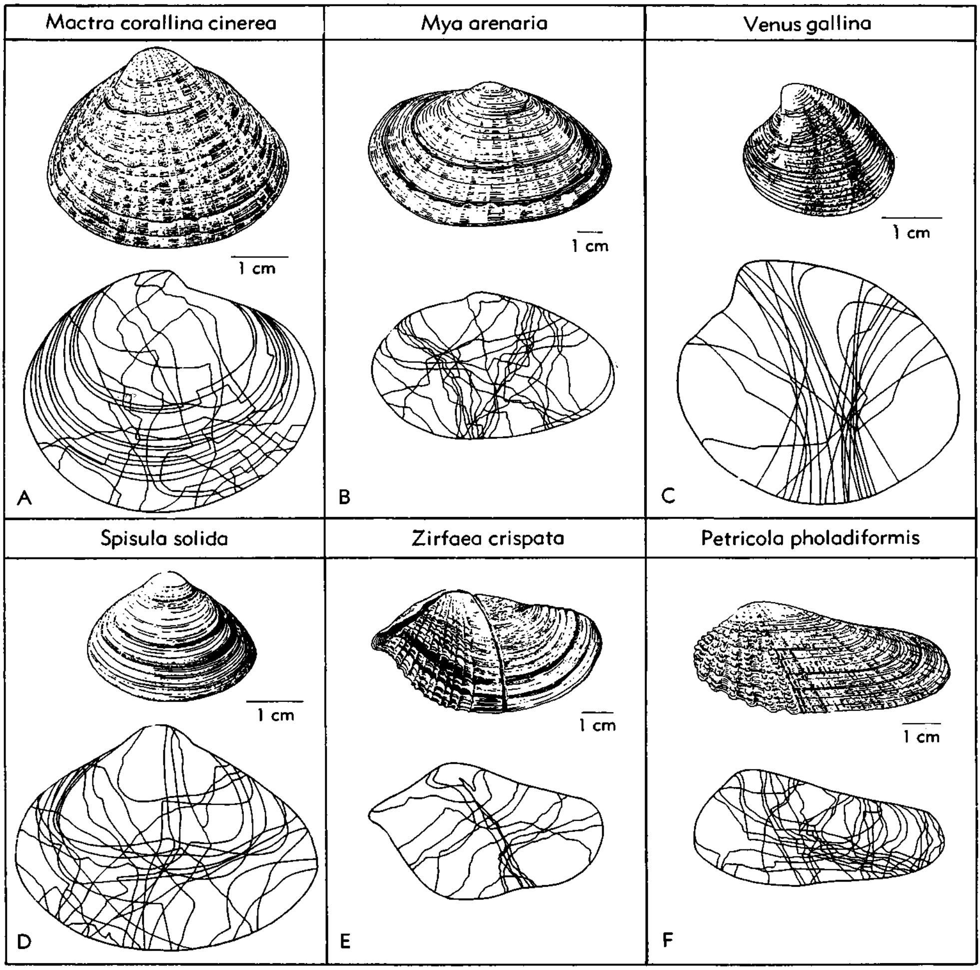


Fig. 16. Fracture patterns developed in different types of recent bivalve shells *(A-F),* strand line deposits from Scheveningen and Kattwijk, Netherlands (Hollmann, 1968b).

ribs generally break parallel to the ribs. Examples are shells of *Cardium echinatum* and *C. edule* (Fig. 15,*A*,*B*). Fracture will be perpendicular to weakly developed radial ribs, as in shells of *Venus gallina* (Fig. 16, *C*). Forms with strongly developed growth lines tend to fracture parallel to the growth lines (i.e., *Mactra corallina*, Fig. 16,*A*). Oval-shaped or arched fracture patterns are common in forms such as *Spisula* (Fig. 16,*D*). Transverse fractures and curved fractures with sharply defined boundaries cut across the umbonal regions of shells of *Mactra corallina*, but bypass those of shells of *Spisula*. Thin-walled bivalve shells with distinct, concentric growth lines commonly break along the growth lines. Small rings remain, which, at first glance, resemble anchor-facets. *Ostrea* shells break along the shell margins and are progressively worn away until only the ligament area remains. Cracks in the shells of *Mya arenaria* and *Scrobicularia plana* follow the prismatic layer along the growth lines. The left valve of *Mya* (Fig. 16,*B*) will splinter and produce wavy or serrated lines of fracture, essentially in the ligamental groove. Generally, splintery, ragged, or wavy fractures prevail. In such forms as *Pholas dactylus, Cyprina islandica*, and many other bivalves, destruction of the shells is so complete that only the hinge areas remain. The shells of elongate thin-shelled forms such as *Ensis, Barnea*, and *Petricola pholadiformis* (Fig. 16,*E,F*) break along the most strongly arched parts. Shells of *Mactra subtruncata* and *Macoma baltica* seldom break in this manner, and those of *Donax vittatus* almost never do. Species differ in regard to the strength of their hinge and umbonal areas and these parts are often found in rich concentrations.

The destruction of gastropod shells frequently begins with breakage of the aperture and a flattening of the whorls. Details of the process of destruction depend on sculpture and thickness of the shells. As a rule, the especially resistant apertures of shells of *Nassa, Murex, Buccinum*, and similar forms are preserved. Columellas are among the especially resistant parts and may be preserved even when washed around for some time by the surf. In short, conical shells like *Littorina* and *Lunatia*, the apex is commonly the most resistant part. Small breakages can be enlarged to "spiral facts" along the areas of greatest curvature of the whorls and can extend across several whorls (Hollmann, 1968b).

Echinoid tests break up along irregular fractures as long as the epidermis and spine muscles are still preserved. When decomposition of the soft tissues is complete, the tests break up along the sutures, especially along the ambulacral and interambulacral areas.

Among crustaceans, especially those having durable carapaces, only the hardest and most compact parts commonly remain under conditions of turbulence. For example, in lobsters, the rostrum with parts of the cephalon and eye sockets, the mandibles, the clawed extremities of the dactylus, the single clawed teeth of the chelae, the ventral, thorned segments of the abdomen, and the basipodites of both uropods are commonly preserved (Schäfer, 1962; 1972).

SELECTIVE DISSOLUTION OF HARD PARTS PRIOR TO BURIAL

Skeletal material is commonly destroyed prior to burial by selective dissolution. In sea water, this happens under conditions of supersaturation with respect to calcium carbonate. The normal compensation depth, at which calcareous skeletal material enters solution, lies at about 4,000 meters. At this depth, increased hydrostatic pressure and low temperatures result in a high concentration of dissolved carbon dioxide. The corrosion of calcium carbonates in water where $CaCO_3$ is precipitated fluctuates with pH (7.7 to 8.3) (Cloud, 1962), and this is thought to be partially related to the liberation of carbon dioxide by plants during the night. The solubility of calcium carbonate increases with salinity and decreases with temperature. The compensation depth in the Antarctic Ocean is only 500 meters (Kennett, 1966). Calcareous skeletons of microfossils may be partially or completely dissolved in living animals (Jarke, 1961). This process is known as subsolution (Hollmann, 1962, 1964) and can result in all stages of preservation from "ghosts" to complete destruction (Richter, 1931). No compensation depth is known for siliceous skeletons.

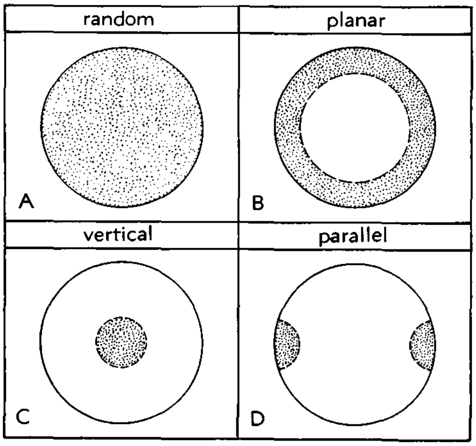


Fig. 17. Diagrammatic representation of orientation patterns (*A-D*) as they appear in stereographic projections (Toots, 1965a).

RANDOM EMBEDDING

Random embedding occurs when objects display no preferred orientation (random orientation). If their distribution is plotted as a stereographic projection, no particular orientation is evident (Fig. 17,*A*).

Random embedding has received very little notice in the literature. Generally, it was regarded as a matter of course and was thought to have occurred under conditions of quiet sedimentation. Toots (1965b) first proved this assumption to be

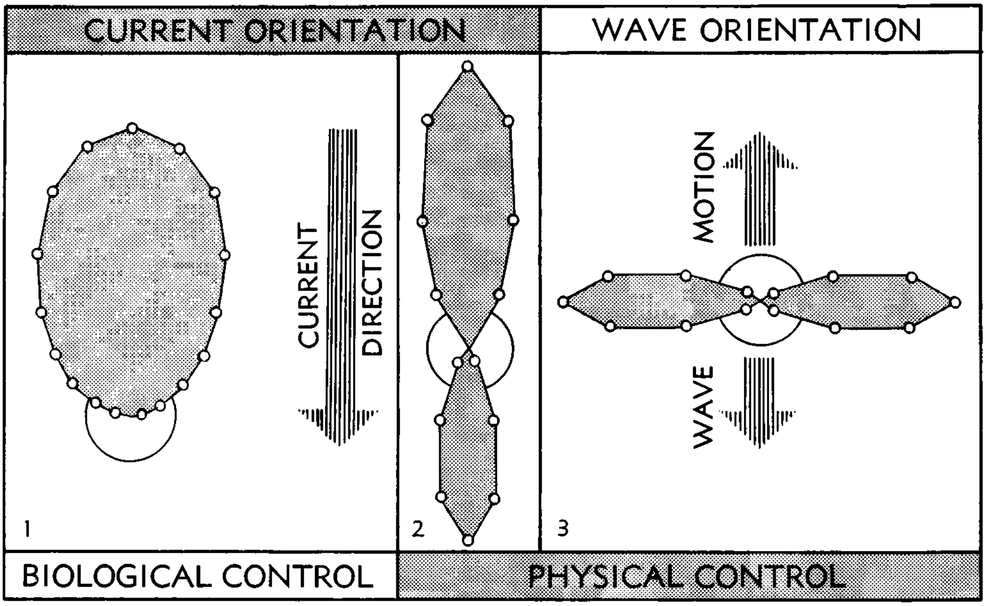


FIG. 18. Orientation of organisms within bedding plane. Arrow designates current direction for *1* and *2*.——*1*. Biologically controlled current orientation: suspension feeders are oriented with only a broad peak into direction of current.——*2*. Physically controlled current orientation: elongate particles arranged so that a sharp major peak points into the current and a smaller counterpeak in the opposite direction.——*3*. Transverse wave orientation: elongate particles aligned with two equal peaks perpendicular to wave movement and occasional smaller peaks parallel to wave movement (after Seilacher, 1973).

incorrect and demonstrated that the process requires special interpretation. Random orientation may result under the following conditions:

1) If organic remains are caught in steep-walled pockets, which act as traps, this results in primary random embedding. But the evidence for this is not unambiguous because gravity plays a part (MÜLLER, 1951b; RICHTER, 1942; TOOTS, 1965a,b).

2) Comparatively rarely, contemporary deformation may be due to a plastic flow of the entire sedimentary mass.

3) Bioturbation. The degree of reworking is dependent upon the size, type, and number of infaunal elements and the time spent in reworking the sediment (MÜLLER, 1951b; QUENSTEDT, 1927; RICHTER, 1936; REINECK, 1967).

ORIENTED EMBEDDING: MOVEMENT AROUND HORIZONTAL (EINKIPPUNG) OR VERTICAL AXES (EINSTEUERUNG)

The types of movement of different media (water, ice, air, mud, or flowing sand) determine the movements of enclosed objects. Such movements can lead to oriented embedding. For example, oblong objects can be oriented either parallel or perpendicular to currents (Fig. 18). The orientation of such objects depends only upon conditions of equilibrium and friction, not upon the original life positions of the organisms. The preservation of fossils and the deposition of them in a fixed position enables conclusions to be drawn about the direction of their movement and final deposition. From this information, it is then possible to determine the direction of the depositing water or wind currents. Such interpretations can be reinforced by the study of independent evidence. This evidence can be sedimentologic (sedimentary structures or the alignment of coarse-grained sedimentary particles). It is also possible to observe the reactions of animals to currents, such as the rheotactic alignments of lebensspuren (SEILACHER, 1953, fig. 5) and the growth orientations of epizoans (SEILACHER, 1960b; MÜLLER, 1963) and certain types of borings (SEILACHER, 1968b; 1969) (Fig. 18).

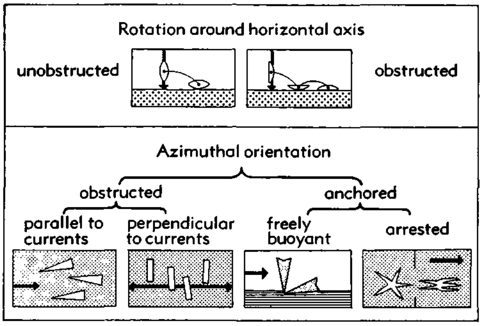


FIG. 19. Types of oriented embedding of skeletal material (after Geyer, 1973). See also Table 4.

On the other hand, it is possible to observe the effect of currents on objects that have sunk into the sediment or are only stuck in the sediment. In either case, objects will acquire the most stable position possible in relation to the forces acting upon them.

As a rule, intraformational folding results in rotation of incorporated fossil remains around a horizontal axis; however, in such cases differential movements often take place. The resulting movements can be very complex and rotation may occur around the vertical as well as inclined axes. Rotation can develop through differential, local carbonate dissolution within the sediment causing settling of the sediment. These and similar processes that result in oriented positions are called oriented embedding (*Einregelung*) (MÜLLER, 1951b; RICHTER, 1942; SHROCK, 1948; TOOTS, 1965a). Current mechanics have been applied to the study of oriented embedding of skeletal hard parts by investigators such as TRUSHEIM (1931), JOHNSON (1957), BRENCHLEY and NEWALL (1970), ABBOTT (1974), and FUTTERER (1974, 1977).

Following RICHTER (1922; 1937; 1942), two major categories of oriented embedding are recognized: *Einkippung* (rotation around a horizontal axis) and *Einsteuerung* (rotation around a vertical axis or azimuthal orientation). Within these categories, a number of subcategories have been defined (Fig. 19, Table 4). Stereographic diagrams are used to record the positions of specific assemblages (Fig. 17,*B-D*). This facilitates the recognition of combinations and transitions of the basic types of embedding described above.

Oriented embedding of bowl-shaped objects. Bowl-shaped objects are common as fossils. Most of them are the shells of brachiopods, bivalves, gastropods, and also arthropods, especially trilobites and crustaceans. Among brachiopods and bivalves, only single valves are, as a rule, truly bowl shaped, but in certain concavo-convex or plano-convex forms (e.g., many strophominids), the entire shell is bowl shaped. We shall first consider the case of *Einkippung.*

If shells sink freely through quiet water, they will be oriented convex side downward (CLIFTON, 1971). A similar orientation will result if shells settle freely through the air, but the aquatic medium is more important geologically. Under conditions of free sinking, the following conditions of free *Einkippung* have been observed:

1) Skeletal parts of dead animals, attached to seaweed or free living, which were pseudoplanktonically transported;

2) Bowl-shaped shells that, once settled, were stirred up by currents and then sank again;

3) Bowl-shaped objects washed up against resistant objects will eventually drift across the obstruction and settle in quiet water on the lee side. In German, this is called *Stillwasserfallen* (still water traps). Two types of orientation can result from *Stillwasserfallen.* Whether the resulting position of the shells is convex side down or arranged in random orientation depends upon the inclination and roughness of the sediment surface, and whether the object is moved by rolling, shoving, or sinking.

Convex-side-down orientations can normally be maintained only in quiet water, in the absence of sufficiently strong, lateral currents. Only shells with a low center of gravity may remain in this position also in the presence of stronger currents. An example from the fossil record is the carapace of *Triarthrus eatoni* described by BEECHER (1894) from the Ordovician of New York, which was found convex downward in an orientation similar to the life position of certain brachiopods and bivalves.

Bowl-shaped shells, whose morphology approaches that of a calot, can be tilted by currents if they are lying convex downward on the sediment. If such tilting occurs

TABLE 4. *Different Types of Shell Orientation (prepared from Richter, 1942).*

<table>
<tr><td colspan="4">A. Orientation with respect to the horizontal axis (<i>Einkippung</i>)
This type of orientation results when objects are rotated around a more or less straight axis and become inclined. Characteristic of different processes and can be divided into the following two groups:</td></tr>
<tr><td colspan="2">1. "Unobstructed" Inclination</td><td colspan="2">2. "Obstructed" Inclination</td></tr>
<tr><td colspan="2">Results when bodies are to move freely in a medium solely under the influences of hydrodynamic resistance, gravity, and buoyancy. They then can sink unobstructed to the bottom.
Example: Bivalve valves sinking to the bottom of a body of water.</td><td colspan="2">Results when shells are under the influence of sufficiently strong lateral currents acting upon the surface of another medium with a higher density, such as water moving over sediment.
Example: Plasters of bivalve valves oriented in the convex-up position.</td></tr>
<tr><td colspan="4">B. Azimuthal Orientation <i>(Einsteuerung)</i></td></tr>
<tr><td colspan="4">This type of orientation occurs when shells are rotated around their vertical axis, and on flat or fairly flat surfaces, this can result in a right-left orientation. Azimuthal orientation can be divided into two basic groups:</td></tr>
<tr><td colspan="2">1. "Unanchored" Azimuthal Orientation</td><td colspan="2">2. "Anchored" Orientation (Pivotal Orientation)</td></tr>
<tr><td colspan="2">Resistance to motion is influenced only by the natural hydrodynamic drag of the bodies, and that determines the orientation.</td><td colspan="2">Results with anchored or attached objects whose point of anchoring is within or outside the body.</td></tr>
<tr><td>a) freely buoyant</td><td>b) hindered</td><td>a) freely buoyant</td><td>b) hindered</td></tr>
<tr><td>Freely moving within a medium.</td><td>Resting on the ground or the sediment, either in one place or sliding along.</td><td rowspan="3">Organisms growing together or hanging from one another.</td><td rowspan="3">Resting on the ground or the sediment, either in one place or sliding along. Sliding of the object results in the orientation of the shells which acts the same as anchoring.</td></tr>
<tr><td colspan="2">Dragging</td></tr>
<tr><td colspan="2">Results when an object is not completely lying on the bottom. A condition results that lies in between buoyancy and sliding, and is therefore between hindered and unhindered.</td></tr>
</table>

when the shells are in contact with a hard substrate, it is said to be obstructed (*gehemmt*). This can happen on land caused by wind, but occurs most frequently in turbulent water. In water-laid deposits, the convex-side-up orientation of shells is, therefore, one of the most important criteria for turbulence and should be considered the rule. RICHTER (1942) called it *Einkippungsregel* (Fig. 20). Often the orientation of shells can be used to clarify difficult stratigraphic and tectonic problems, especially for the recognition of overturned position of strata. REINECK *et al.* (1967) have demonstrated with the help of box cores that convex-side-up orientation is also predominant in deep parts of the North Sea. The same is true for empty bivalve valves on the continental shelf (EMERY, 1968).

As a rule, weakly curved, bowl-shaped objects are stable convex side up, but stongly curved, almost high-spired, bowl-shaped objects are most stable convex side down. Examples can be found in the fossil record. Callovian specimens of *Gryphaea dilatata* found redeposited in recent strandline deposits near Houlgate are generally oriented convex upward, according to the *Einkippungsregel.* Convex-side-down orientation, as observed for bivalved shells and also those of *Exogyra columba* in the Cenomanian of Saxony, have retained their life positions (PFANNENSTIEL, 1930; HÄNTZSCHEL, 1924).

Azimuthal orientation of bowl-shaped bodies is most often found under water, but it can also be observed subaerially and perhaps even in more viscose substances such as soft mud. The orientation depends upon the degree of streamlining of the body. The shape of the object determines the hydrodynamic drag and the direction in which it will be oriented. Azimuthal orien-

FIG. 20. Plaster of bivalve shells composed essentially of single valves of *Costatoria goldfussi* (VON ALBERTI) from the lower Keuper (Grenzdolomit) in Thuringia, approx. ×1.1 (Sektion Geowissenschaften, Bergakademie Freiberg, 249/2; Müller, n).

tation is best developed when shells have a long and a short axis and are aligned along that axis. Teardrop-shaped objects are best suited to attain azimuthal orientation.

Unobstructed azimuthal orientation has not yet been observed geologically. Possibly it could occur in terrestrial muds and flowing sands or in submarine slides. Obstructed azimuthal orientation occurs when bodies lie upon hard substrates where their transportation is slowed down by friction. In such circumstances, the thickest part of the shell is oriented against the current, although occasionally, and completely unexpectedly, the opposite orientation can occur. Trusheim (1931) performed flume experiments with shells and observed that their orientation may be influenced by minute differences in shape that are often difficult to observe and may even be destroyed during fossilization. Such differences in orientation were observed for single valves of *Cardium echinatum* and *C. edule*, and of *Mactra corallina* and *M. solida*. Futterer (1974) studied azimuthal orientation of single valves of recent *Cardium edule* and *C. echinatum* in a flume. These experiments were concerned with the orientation of the shells in relation to changing centers of gravity and it was discovered that a shift of the center of gravity by a few millimeters can lead to very different, opposing orientations of the shells. Apparently, minute differences in shell shapes are important, and it is possible to distinguish different species by the manner in which they are oriented. A considerable amount of caution must therefore be taken when applying results obtained on recent material to the study of fossil conditions. Generally, other criteria than shape should be used. Different modes of orientation of bowl-shaped shells are illustrated in Figure 21, in which rose diagrams and orientation quotients for different biotic constituents of shell plasters in the upper Buntsandstein are compared.

Right and left valves of more or less equivalve bivalves commonly show azimuthal orientations in opposite directions (see also Fig. 22). Even if both valves of a bivalve shell are held together by the ligament, azimuthal orientation can still result. However, such occurrences can only happen if both valves can move with respect to one another and if they lie convex side up on the sediment.

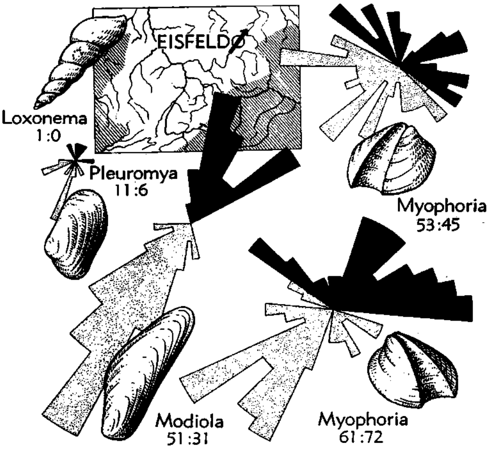


Fig. 21. Rose diagrams and ratios of single valve azimuthal orientations in shell plasters, Lower Triassic (upper Buntsandstein, Röt), Eisfeld, Thuringia, approx. ×0.5 (Seilacher, 1960a).

1) The shells of *Mytilus, Modiola, Arca, Venerupis, Petricola, Ensis, Phaxas*, and *Donax* are oblong, and their hinge parts are straight. Therefore, these shells behave like sled runners with the shell edges lying flat on the substrate and the umbo pointing toward the current.

2) The shells of *Cardium, Scrobicularia*, and *Mactra* have rounded outlines and even when gaping widely, rest on only one of the valves, while the other valve points upward like the open lid of a can. The umbonal region, being heaviest, always points toward the currents.

It has been observed in nature and with controlled experiments that the thickest end of the shell is positioned against the current. For single bivalve valves, this means that the umbonal region points toward the current. Therefore, this kind of orientation can be used to determine current directions. The situation is different for shells that are embedded convex side up. Bowl-shaped shells with projections or spines that extend over the base of the shell or its margin may be anchored if the substrate is suitable. The anchor always points toward the current. Thus, anchored shells can also be used to determine current directions.

The different conditions of oriented embedding for complete shells and single

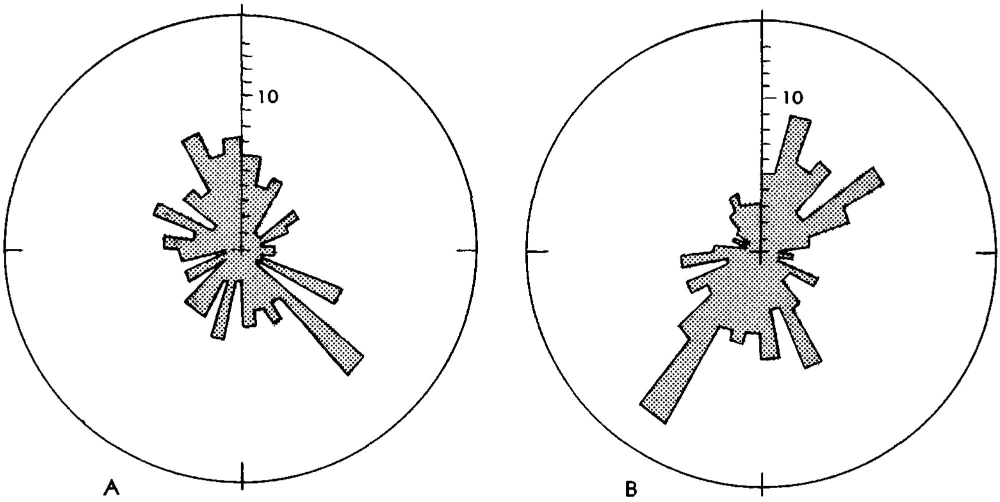


FIG. 22. Rose diagrams for 302 azimuthally oriented, convex-up, embedded single valves of *Costatoria goldfussi* (VON ALBERTI), from the lower Keuper (Grenzdolomit, Ku2) at ?Reisdorf, Thuringia (Müller, n).——*A*. Relationships of 149 left valves (=47.6%).——*B*. Relationships of 153 right valves (=52.4%). Compare with Figure 20.

valves of *Schizothaerus nuttali* and *Protothaca staminea* that were exposed to fluctuating current directions and speeds in muddy sands are shown in Figures 23 and 24. The orientation of concavo-convex particles deposited from experimental turbidity currents is shown by MIDDLETON (1967).

Oriented embedding of cone-shaped bodies. Cone-shaped shells of fossil and living organisms are commonly preserved in sediments. Examples are found among oblong foraminifers, tentaculites, volborthellids, belemnites, styliolinids, conularids, high-spired gastropods, and orthoconic ectocochlian cephalopods. Examples are also found among vertebrate remains. Tilting (*Einkippung*) will be considered first. This is called "unobstructed" if shells are transported without contact with the ground or other substrates such as air, water, and very soft, muddy, or sandy sediment, under the influence of only the shape of the shell, gravity, and buoyancy. In general, we are then concerned with orientation perpendicular to the smallest cross section of the object. If conical objects sink freely, they commonly become oriented with the heavy, basal portion of the shell pointing downward; however, if the surrounding medium is viscous and the height of fall too small, this type of orientation will not result.

Examples of unobstructed oriented embedding of conical fossils can only be observed in sediments of sufficient density and strength to preserve the evidence. Such sediments must be so thoroughly saturated with water that shells can sink in them with their long axis vertical and short axis horizontal. If the sediment becomes more cohesive, this position is retained. In some cases, the orientation of the fossil is in the life position. Probably, the shells of cerithiid gastropods, preserved with the apex pointing downward in unbedded, fine-grained sandstones of the Sarmatian of Wiesen (Burgenland), can be considered as an example (KREJCI-GRAF, 1932). It is assumed that these high-spired gastropods were aligned by currents in flowing sands, and were kept in this position when the sand consolidated.

Obstructed, oriented embedding of conical objects results when horizontally acting forces interact with the objects that are in contact with the substrate, when the cone height is less than the diameter of its base.

Examples can be found in the patellids,

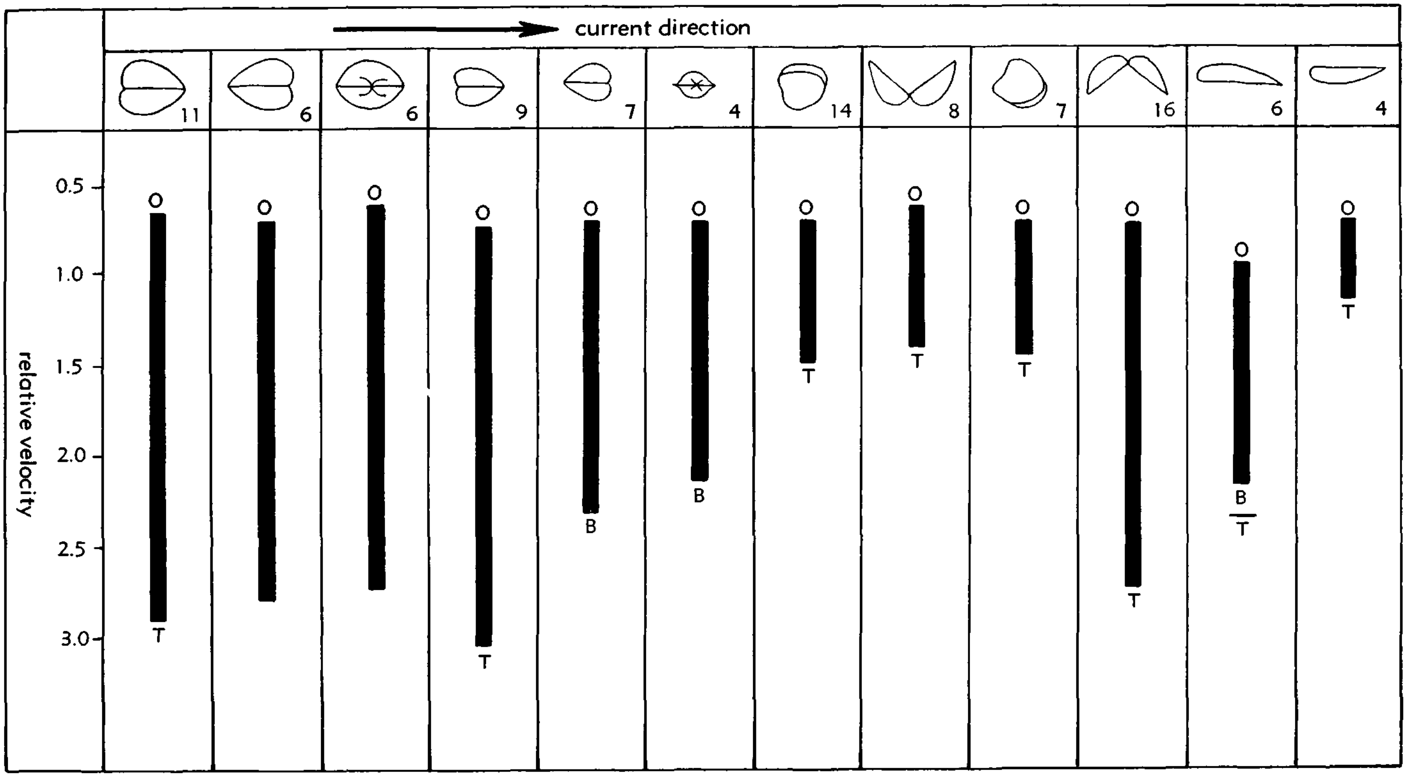


FIG. 23. Reaction of complete shells and single valves of recent *Schizothaerus nuttali* and *Protothaca staminea* exposed to differing conditions of current directions and velocities in muddy sediments (modified from Johnson, 1957). [Explanation: *O*, sand begins to move near the shells; *B*, sand covers the shells; *T*, the shells begin to move. Numbers near the margins of the shells indicate the number of times the experiment was carried out for each shell.]

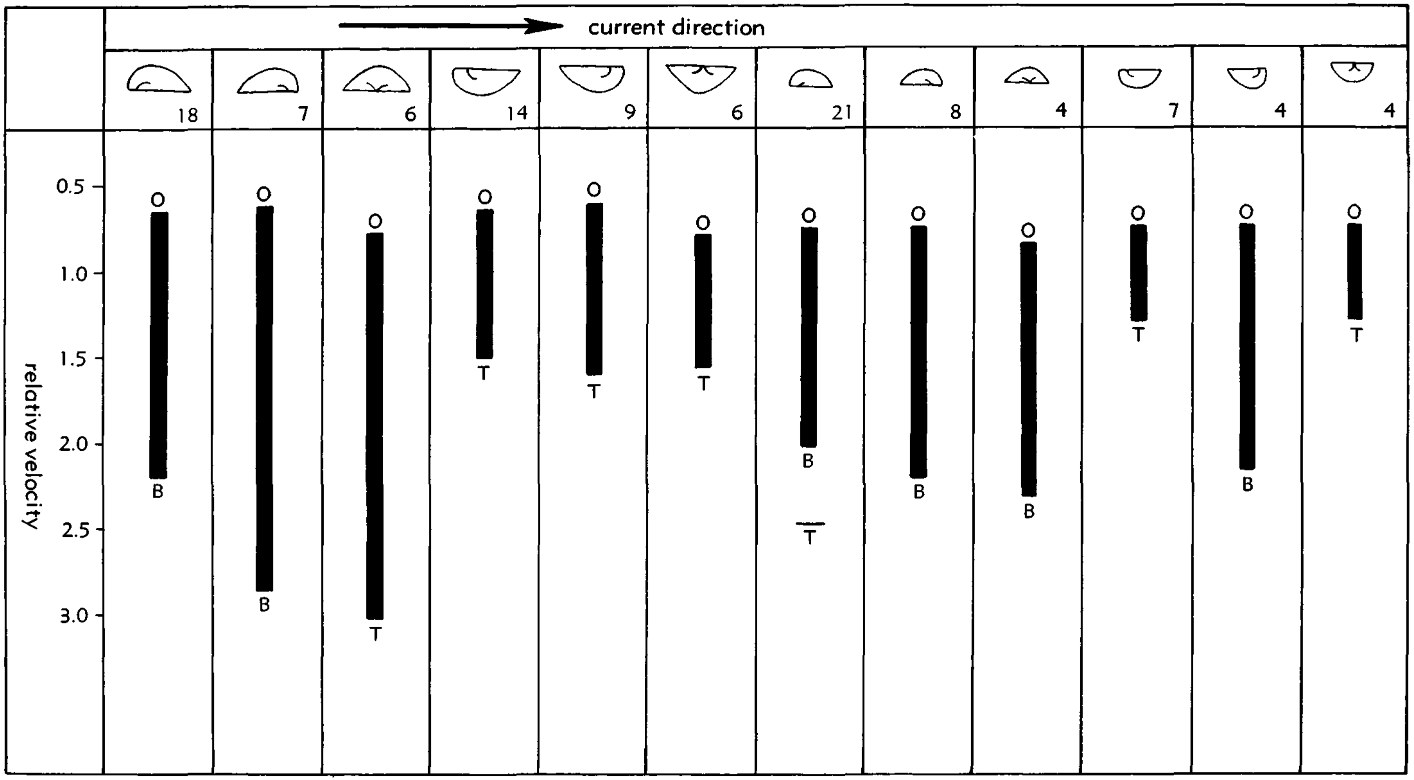


FIG. 24. Reaction of complete shells and single valves of recent *Schizothaerus nuttali* and *Protothaca staminea* exposed to differing conditions of current directions and velocities in muddy sediments (modified from Johnson, 1957). [Explanation: *O*, sand begins to move near the shells; *B*, sand covers the shells; *T*, the shells begin to move. Numbers near the margins of the shells indicate the number of times the experiment was carried out for each shell.]

discinids, and trochids. Shells of *Trochus* can become abraded to such an extent that only the apices remain. Frequently all that remains of gastropod shells with large apertures such as *Murex, Buccinum, Purpura,* and *Aporrhais* are small cap-shaped or "ear"-shaped structures.

The orientation by currents of high-spired, conical objects in which shell height is greater than base diameter is such that their long axes are parallel to the direction of the currents (*Längs-Einsteuerung*). Rose diagrams of such orientations commonly show the presence of two statistical maxima. As a rule, one of the maxima will be much larger and oppose the other. This suggests that even under conditions of unidirectional flow, transported objects are dynamically active and constantly change their orientation from spire upstream to spire downstream and vice versa (Fig. 25). Transverse wave orientation is characterized by two equal peaks, sometimes with an additional smaller peak in the direction of wave progression (Seilacher, 1960a) (Fig. 18,*1*).

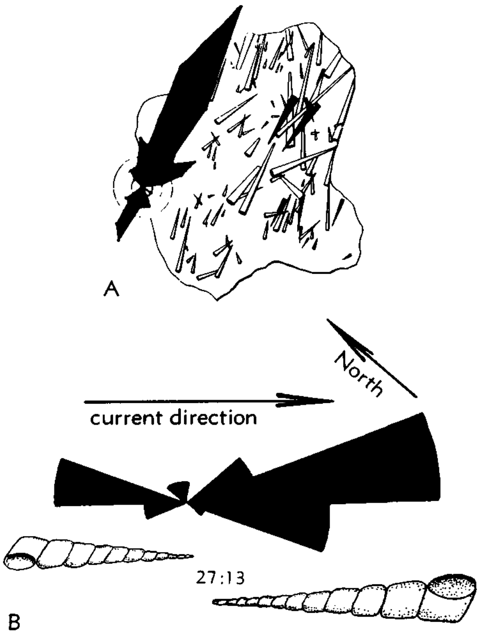


Fig. 25. Orientation of cone-shaped bodies.——*A*. Azimuthal orientation of orthoconic nautiloids from Upper Devonian (Kellwasserkalk), Bicken, Rhineland; approx. ×0.4 (Seilacher, 1960a).——*B*. Rose diagrams for the orientation of 40 gastropod shells (*?Turritella* sp.) in cross-bedded sandstone from Upper Cretaceous (Mesaverde Formation), Carbon County, Wyoming (Toots, 1965a).

Krinsley (1960) studied the azimuthal orientation of 106 orthoconic nautiloids on a bedding plane of the Middle Silurian Waukeshaw Limestone near Lemont, Illinois. The orientations of the nautiloids were plotted in 20 degree classes as shown by rose diagram in Figure 26. Two directions of orientations are obvious, a dominant west-northwest direction and a secondary one at right angles to the first.

Possibly the shells were transported by strong currents and the apices became embedded in the sediment, thus being protected from mechanical erosion and subaqueous solution. Strong currents must have played a large role as shown by the overturning of coral colonies. Krinsley concluded, therefore, that predominant winds and currents from west-northwest were responsible for this orientation.

Ruedemann (1897) reported parallel, azimuthal orientation of orthoconic nautiloids and monograptids in the Silurian Utica Shale of New York. Drag marks could be seen behind the fossils. The apical ends of the nautiloids and many of the siculae of the graptolites pointed in the direction against the current as was also indicated by drag marks in the prolongation of the nautiloid shells.

Similar parallel orientation of orthoconic nautiloids is known from the Silurian Budany Limestone of Czechoslovakia. The celphalopods of the Devonian Hlubočepy Limestone, on the other hand, show two dominant directions of orientation at right angles to each other. In the latter case, the orientation was thought to have been caused by cross waves and low velocity currents (Petránek & Komárková, 1953). Kay (1945) observed two directions of orientation for Ordovician orthoconic cephalopods on St. Joseph Island, Ontario, and Cumberland Head, Vermont. The smaller shells were generally aligned at right angles to the larger ones. Kay suggested that the larger shells were oriented perpendicular to the

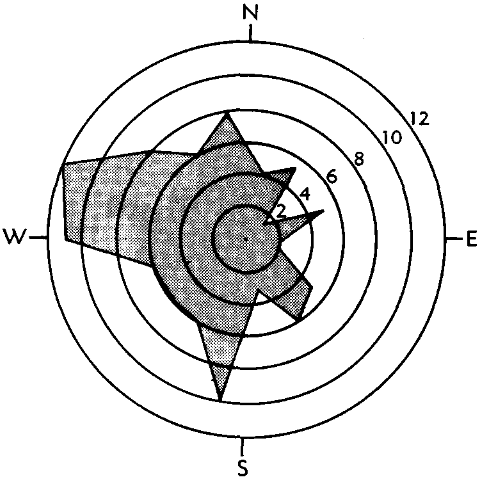


FIG. 26. Rose diagram showing the azimuthal orientation of 106 orthoconic nautiloids along a bedding plane; specimens from Middle Silurian, Lemont, Illinois. The apical ends point in the indicated compass direction (Krinsley, 1960).

shoreline and the smaller ones parallel to it. Other examples of orientation of conical shells have been discussed by KINDLE (1938), RUTSCH (1937), TRUSHEIM (1931), REYMENT (1968), DIXON (1970), K. BRENNER (1976), and FUTTERER (1976, 1977).

Only few examples of embedding and orientation of high-spired, conical bodies perpendicular to the current direction have been described in the literature. SEILACHER (1960a) studied the distribution of the foraminifer, *Haplostiche*, on ripple-marked bedding planes. The long axes of the foraminifers were observed to lie parallel to the ripples as shown in three separate rose diagrams in Figure 27. The orientations of the shells displayed two large and opposing maxima, which were interpreted to represent the most stable positions. SEILACHER considered the deposit to be an example of wave orientation (*Quer-Einsteuerung*). Another example would be the well-known mass occurrences of belemnites (*Schlachtfelder*) where the rostra are oriented perpendicular to the current (QUENSTEDT, 1927; SEILACHER, 1960a). GEKKER (1957, pl. 2, fig. 3) has figured a remarkable example of tentaculites from the Upper Devonian of the USSR that display the same orientation. Possibly the latter orientation was the result of the mechanical interaction of shells as they were deposited along the shoreline.

An example of wind-oriented gastropod shells as indicators to determine paleowind directions has been documented by ERICKSON (1971).

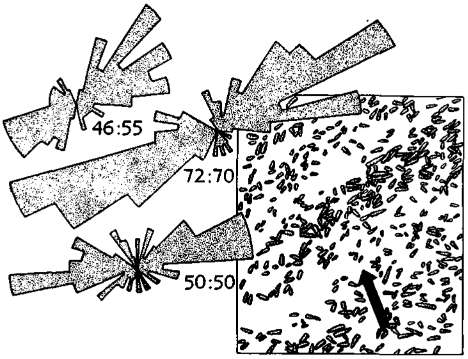


FIG. 27. One of the few known cases of conical bodies (*Haplostiche* sp.) oriented with their long axes perpendicular to the current direction (indicated by arrow). Preserved on the lower surface of a ripple marked bed, from Lower Cretaceous, Texas, ×0.7 (Seilacher, 1960a).

Oriented embedding of barrel-shaped bodies. Elongate, barrel-shaped bodies in contact with a substrate will roll under the influence of currents and become oriented with their long axes perpendicular to the direction of the current. Of course this can occur only under ideal conditions where both the substrate surface and the barrel-shaped bodies are smooth. If the substrate is uneven, the rolling bodies are obstructed or anchored to the substrate. This is the most common condition, as perfectly smooth substrates rarely exist in nature. Slight differences in relief of the substrate may obstruct or impede the movement of bodies, which may become anchored and then pivot around the anchoring point, thus becoming oriented more or less parallel to the transporting current.

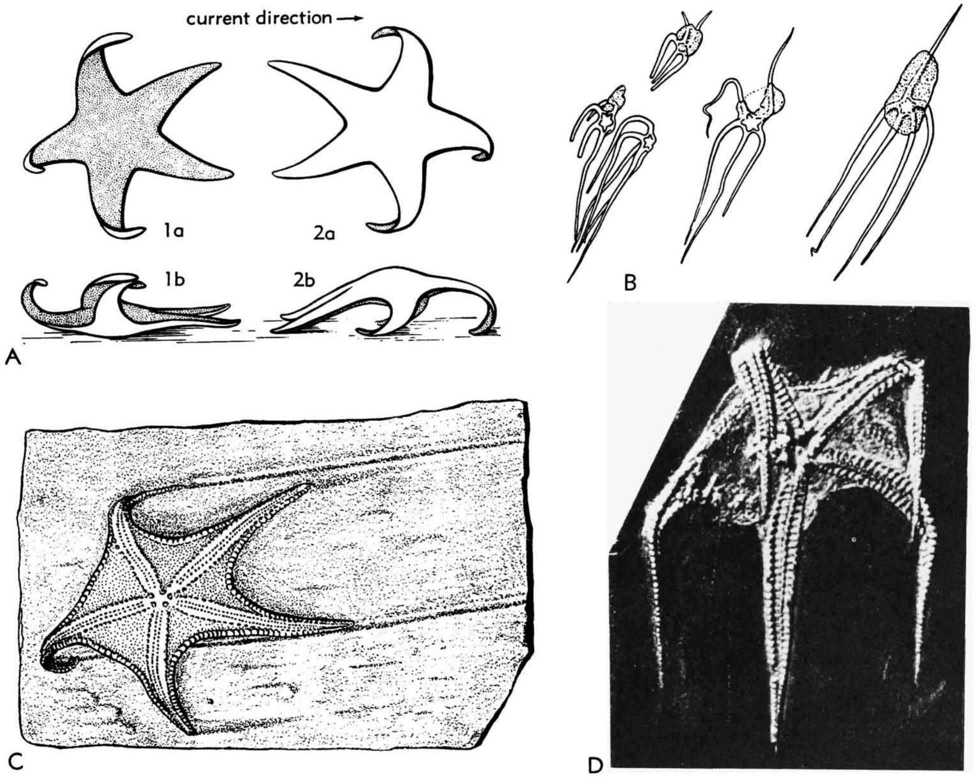


FIG. 28.——*A*. Two possible azimuthal orientations for dead starfish (Seilacher, 1960a).——*B*. Azimuthal orientation of tests of *Furcaster* transported by currents, after partial decomposition, Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhineland, approx. ×0.23 (Seilacher, 1960a).——*C*. *Euzonosoma tischbeiniana* (ROEMER) in "umbrella" position. The straight grooves are tool marks produced by the drooping arms. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhineland, ×0.36 (Seilacher, 1960a).——*D*. *Euzonosoma tischbeiniana* (ROEMER) displaying azimuthal orientation and the beginning of rotation around a horizontal axis. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhineland, approx. ×0.54 (von Königswald, 1930).

The orientation of these objects in water is always parallel to the shoreline. Most common examples of this type are seen in plant material (branches, pieces of tree trunks, chaff); however, random orientation can also occur.

The orientation of rod-shaped coprolites has been interpreted to demonstrate the presence or absence of waves during deposition of the Upper Pennsylvanian Rock Lake Shale in northeastern Kansas (HAKES, 1976). Wave-oriented coprolites were found to be aligned essentially parallel to ripple crests, whereas coprolites deposited in areas of little wave activity were found to be randomly oriented within bedding planes.

Oriented embedding of bodies with long, flexible, or projecting parts. In this category belong echinoderms (asterozoans, crinoids), vertebrates, and plants. Good examples of *Einkippung* are found among fossil asterozoans. Commonly, obstructed embedding of these objects occur if some of the arms are bent back over the central disc. VON KÖNIGSWALD (1930) described two transitional types of embedding of asterozoans from the Lower Devonian Hunsrückschiefer of the Rhenish Schiefergebirge:

1) Initial inclined position: The body does not move, but some of the arms are bent back across it (Fig. 28,*A*,*C*,*D*).

2) Final position: In addition to the

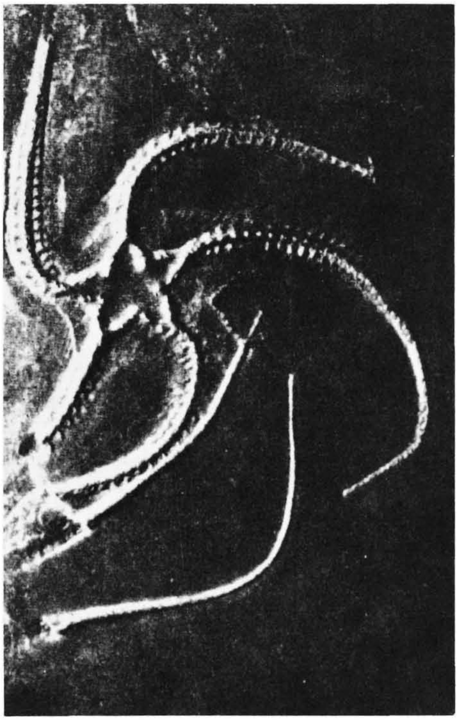


FIG. 29. *Furcaster palaeozoicus* STUERTZ in a "twirl" position. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhenish Schiefergebirge, approx. ×1 (von Königswald, 1930).

arms the entire body is moved in the same direction but only for a short distance.

Another type of orientation occurs when the body of a starfish has been carried along by currents, and its arms are dragged over the sediment (SEILACHER, 1960a). Figure 28,*C*, shows drag marks produced by the arms of the animal as straight, parallel furrows. In the specimens of *Furcaster* shown in Figure 28,*B*, the central discs have partly disintegrated and have been moved by the current.

The bodies of starfish are flipped over and tumbled by currents, which accounts for the bending of the arms and their occasional orientation in a direction against the current. Previously this orientation has often been explained as being due to counter (tidal?) currents.

Tentaculites and orthoconic cephalopods do not usually show oriented embedding in the Hunsrückschiefer, which is probably explained by the fact that currents responsible for the transportation and oriented embedding of starfish may be quite weak. As is well known, skeletal elements of echinoderms are composed of a meshwork of calcite crystals having considerable porosity. Therefore, these skeletons have an extremely low specific gravity and can be easily transported by very weak currents that are not sufficiently strong to move other larger and heavier objects. The transportation of echinoderm particles is also facilitated by the entrapment of decomposition gases within their tiny cavities. After embedding, the cavities of the skeletal meshwork are filled in by secondary calcite and each skeletal element becomes one calcite crystal with its own cleavage plane.

Embedding and anchoring of objects are dependent upon the shape of the surface (*Standfläche*) on which they come to rest. This surface is usually small in the case of long, flexible, and projecting body parts such as extremities, tentacles, tails, or necks, which are generally oriented parallel to the current. Commonly they nestle against well-anchored parts, which form a kind of facets ("*Anspülen einer Facette*") (WEIGELT, 1927, p. 119).

Asterozoans commonly display anchored or inhibited azimuthal orientation, if the central disc is firmly anchored in the substrate and only the arms are oriented by currents (Fig. 28,*A,D*). However, if arms are bent over the body of the starfish, this is a form of tilted orientation called "umbrella position" (Fig. 28,*D*). If all arms of starfish are spirally bent in the same direction by currents, this is referred to as *Quirllage* ("twirl position") (Fig. 29). This occurs mainly in forms with long, moveable arms, but is also present in starfish with less well-developed arms. Similarly, the spiral arrangement of distarticulated skeletal elements of *Palaeoniscus* specimens in the Kupferschiefer were apparently embedded by small eddies in rather shallow water.

The orientation of sessile, stalked crinoids can be used to determine current direction. This is especially true if the animals are anchored to the sediment at the time of burial, and if root, stem, and crown are not disarticulated. The animals then become oriented in the direction of the

FIG. 30. *Encrinus carnalli* BEYRICH displaying more or less azimuthal orientation by currents. Middle Triassic (lower Muschelkalk, Schaumkalk Zone), Freiberg a. d. Unstrut, East Germany, approx. ×0.38 (Müller & Zimmermann, 1962).

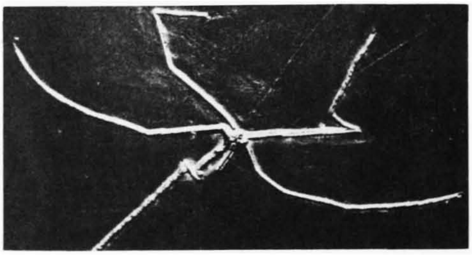


FIG. 31. *Agriocrinus frechi* JAEKEL, stem bent immediately below calyx. Arms diverging 180° caused by reversal of current direction. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhenish Schiefergebirge, approx. ×0.4 (von Königswald, 1930).

current. In fairly strong currents, they are quickly disarticulated; however, if the currents are relatively weak and unidirectional, a progressive alternation of orientation can be developed. Initially, the crinoids are deposited in a tangled, disordered mass, but as current intensities increase, a parallel arrangement will eventually develop (Fig. 30). In the latter case, the stalks are commonly embedded in proximity, parallel to each other on a single bedding plane. The appearance of tangled masses of crinoids in the Liassic *Posidonia* Shale of southern Germany indicates low energy conditions, and the more parallel arrangement of them indicates occasional, stronger currents. If the stalk of crinoids is separated from the bottom, it drags along and acts as a drift anchor.

Instructive examples of the orientation of body parts in different directions due to changing current conditions are known in the Hunsrück Shale (VON KÖNIGSWALD, 1930). For example, the crinoid, *Triacrinus,* has long, rigid arms that were aligned by steady currents in close packing. If the current is reversed 180 degrees, the arms are pushed widely apart (Fig. 31). Because of this, current pressure is increased so that the stalk breaks just below the calyx and the same may happen to single arms, because they are relatively rigid.

Changes in current direction are excellently displayed when several layers of fossils are deposited on top of one another on a single bedding plane. The differences in orientation of the fossils can then be as much as 180 degrees. Commonly, in the first layer the fossils are oriented by the dominant current and their orientation is only slightly changed by later changes in current direction (Fig. 32,*A*,*B*). In graptolite shales, two or, rarely, more layers of oriented graptolites are present, in which the graptolites cross each other at uniform angles.

Rapid changes in current direction are considered to be tidal in origin.

Paleowind directions may be determined by measuring the azimuthal orientation of broken and fallen tree trunks, if they are oriented parallel to each other. This has been found in occurrences within, or stratigraphically above, central European brown coal deposits.

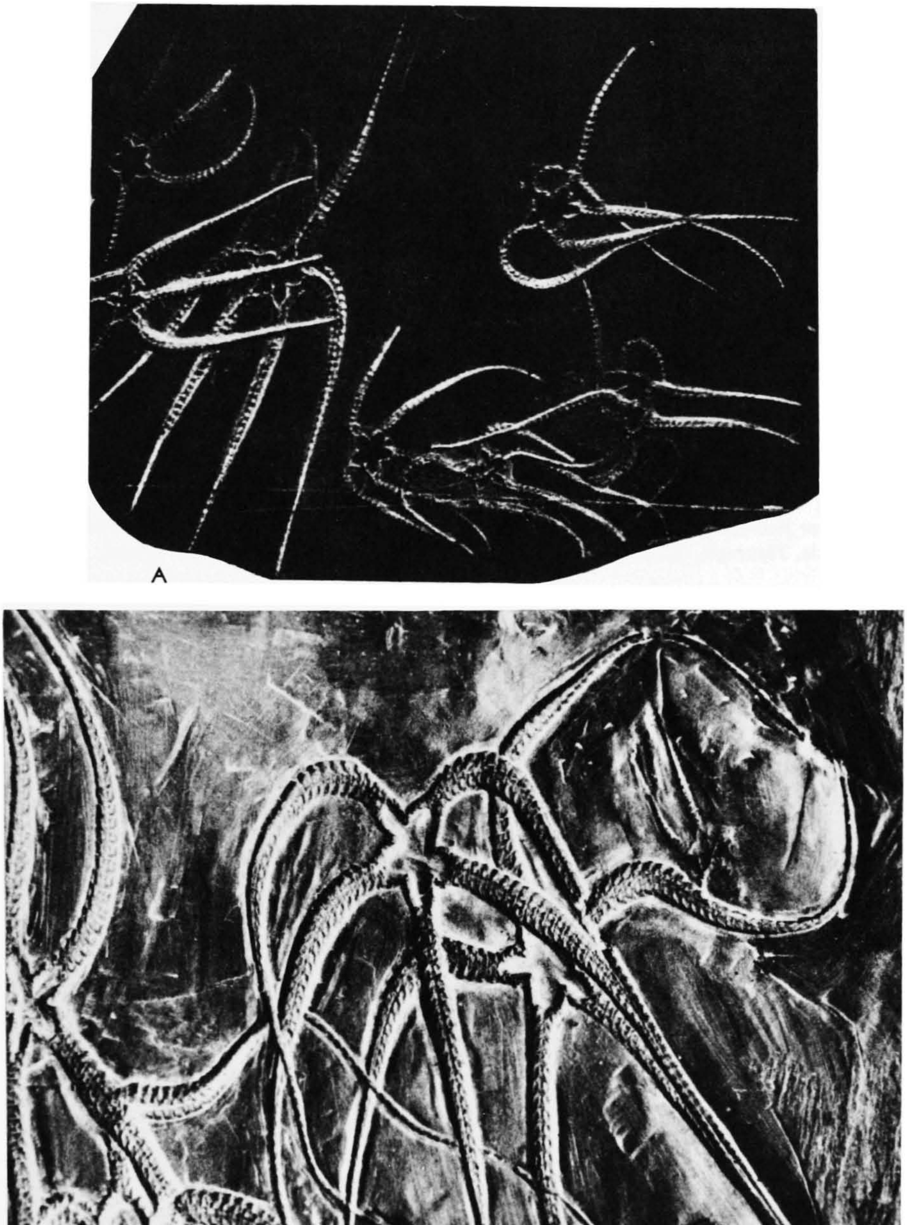
Azimuthal orientation *(Einsteuerung)* of planispiral ammonoids has been studied by BRENNER (1976), and that of *Nautilus* and *Spisula* by FUTTERER (1976, 1977).

Marks in the sediment produced by the remains of organisms. In German, the term "*Marken*" implies inorganic structures produced on substrates by mechanical means. Their development differs from that of lebensspuren (trace fossils) because the forces involved are entirely inorganic. Dead animals or solitary parts of animals can be moved by currents and, when they come in contact with the sediment, produce drag, roll, or prod marks. Their importance is obvious, because, along with other sedimentologic and biostratinomic indicators, they furnish information on nature, direction, and strength of ancient currents. The following are examples.

1) Drag marks (*Schleifmarken*) with chevron-like rills of the "chloephycus" type (Fig. 33) (see HÄNTZSCHEL, 1975, p. *W*171). If objects are dragged across fairly viscose

(See facing page.)

FIG. 32. Examples of orientation by currents.——*A*. Two successive deposits of *Furcaster palaeozoicus* STUERTZ, oriented by two different current directions. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhenish Schiefergebirge, approx. ×0.3 (von Königswald, 1930).——*B*. Arms of *Furcaster palaeozoicus* STUERTZ oriented by currents, from Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhenish Schiefergebirge, approx. ×1.7 (Müller, 1963).


A
B

substrates, small chevronlike wrinkles can result. The points of the chevrons point downcurrent, and they can be used as current-direction indicators. These structures are always found on the bottom of beds, and if other indicators of current direction are associated with them, these structures can be used to interpret the direction of flow.

2) Drag marks of medusae, e.g., *Rhizostomites admirandus* (Haeckel) from the Solnhofen Limestone of southern Germany (Janicke, 1969; Kolb, 1951). The marks shown in Figure 34 originate in the upper right. From that point, as many as six parallel drag marks are developed that continue for about 12 cm. Toward the center of the picture they change into an entangled mass of fine ridges running to the upper left where the outline of part of the medusa's body is found.

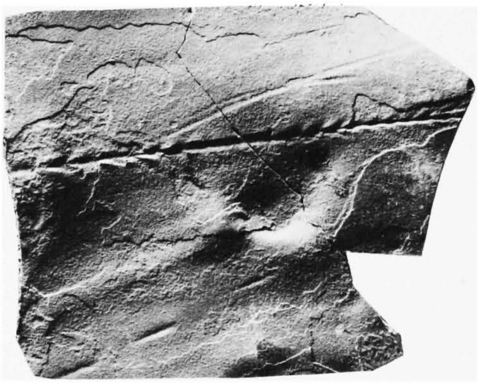


Fig. 33. The drag mark "chloephycus" displayed on an upper bedding plane. The feathery appearance is caused by rhythmic movements of an unknown object along the sediment surface. Lower Permian (lower Rotliegendes, Oberhöfer Schichten), Friedrichroda, Thuringia, ×1.9 (Müller, 1971).

Fig. 34. Drag marks of medusa, *Rhizostomites admirandus* Haeckel, Solnhofen Limestone (Malm zeta, lower Portlandian), Gungolding, Bavaria; width of section, ×0.45 (Janicke, 1969; photo by courtesy of Bayer. Staatssammlung für Paläontologie u. Historische Geologie, München).

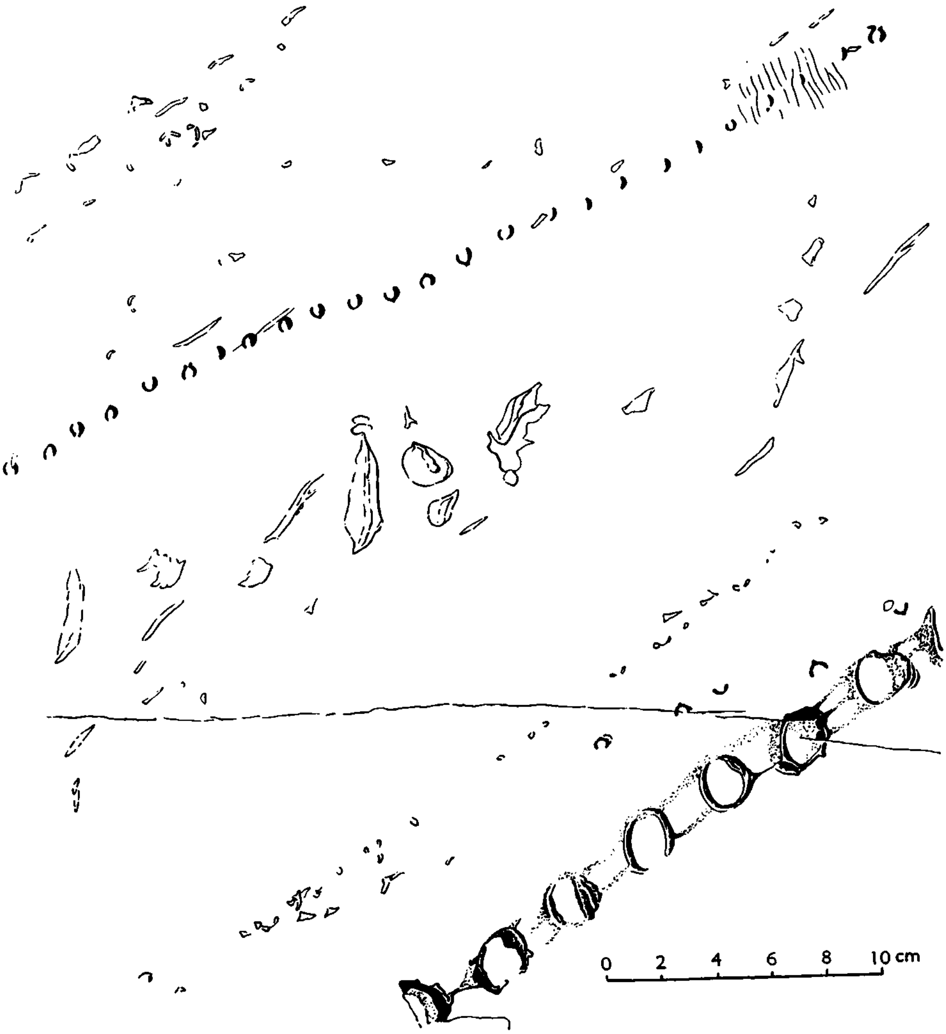


FIG. 35. Roll marks of ?fish vertebrae parallel to the current direction and perpendicular to the trend of the ripples (upper right). Impression of other ?skeletal parts can be seen in the upper part of figure, also aligned with the currents. Oligocene (Flysch), Engi-Matt, Switzerland (Pavoni, 1959).

3) Roll marks of probable fish vertebrae (Fig. 35) in the Oligocene of Switzerland (PAVONI, 1959) and roll marks of ammonite shells that have been moved across the substrate by uniform currents (BARTHEL, 1964; JANICKE, 1969; SEILACHER, 1963).

4) Prodmarks of reeds from the Upper Triassic (Keuper) of Germany (Fig. 36). As with prod marks produced by parts of trilobites, ammonite shells, or fragments of those, the objects were carried by currents, oriented in cross or oblique orientation. The resulting marks on the substrate are depressions, which can be used to indicate the general direction of the carrying currents (JANICKE, 1969; SEILACHER, 1963). In general, the up-current side of these sedimentary structures are flatter than the leeward sides.

5) Changing current conditions can be clearly recognized from marks made by pivoting plant remains (i.e., seaweed, small branches) in anchored azimuthal orientation in both subaqueous (LANGERFELDT, 1935)

FIG. 36. Prod marks produced by reeds, from Upper Triassic (Middle Keuper, Schilfsandstein), Sternenfels, Württemberg; approx. ×0.7 (Linck, 1956).

and continental environments (GERHARZ, 1966; MÜLLER, 1967). The tethered objects produce scraping marks in the sediment, which stand a good chance of preservation. They are rarely observed under water, and are much more common on land where they are formed under conditions of rapidly changing wind directions. Because wind direction can change 360 degrees in a short time, the resulting marks left in the substrate can be circular; however, the predominating wind direction is recognizable from the greater intensity of the scraping marks on the lee side. In the fossil record such marks can be used as additional criteria in the interpretation of paleowind directions.

Such marks produced by plants are extremely common in fine, soft sand and are known to have diameters up to 1.5 m, under as much as 2 cm of water cover (MÜLLER, 1967). Their appearance is extremely variable and simple circular impressions may be found next to entire sets of circles, and smooth areas can be located next to wavy or jagged margins. Sometimes, perfect, wheel-shaped structures of concentric rings are produced. Spokelike structures (prod and drag marks) can result if the winds blow steady from one direction for some period of time. Such circular structures are particularly common along beaches where sea and land breezes alternate daily and in slightly indurated sediments, such as boulder clay. They can also be formed on vertical faces, although they are mostly cut in the sediment by pivoting of parts of plants around an anchoring point under the influence of strong, fairly unidirectional winds (Fig. 37). They can also be produced by the bodies of dead animals, such as fish cadavers which are anchored by their tails, swinging from side to side as described from the Solnhofen Limestone in southern Germany (BARTHEL, 1966).

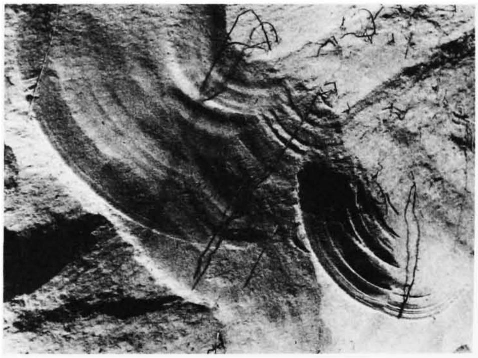


FIG. 37. Circular structures produced on the vertical faces of dune sand by plants blown by winds. Recent example, from Baltic Sea near Wustrow; ×0.25 (Müller, n).

FOSSIL DIAGENESIS

GENERAL DISCUSSION

As sediment accumulates, its increasing weight causes changes in pressure, temperature, and volume which initiate disturbances of the equilibrium that developed between component elements during deposition. This results in rearrangement of constituents until they are again in equilibrium with the surrounding energy conditions. Diagenesis can be defined as the processes acting upon sediment and its constituents from deposition to eventual alteration by metamorphism or weathering. There is no sharp boundary between diagenesis and metamorphism. The same conditions of temperature and pressure that can cause typical metamorphic textures in bedded salt have insignificant effects when they act on limestone. It is just as difficult to draw a line between diagenesis and weathering processes, because the transition is gradual. Once the dead organism and its parts are embedded in the sediment, they become part of it and participate in the diagenesis of the sediment. They undergo alterations, the accurate knowledge of which is important for the proper interpretation of fossils. A study of the older literature reveals that sometimes new "species" were based on products of diagenetic alterations.

According to differences in pressure, temperature, time, and chemical composition of rocks, diagenetic processes progress at very different rates.

For a given sediment, increased deposition tends to continually reduce pore space in the underlying material, and the pore water, except for a very small amount of moisture, is lost through compaction. The composition of this water that migrates upward depends upon that of the surrounding rock and changes generally soon after deposition. Solutions migrate by diffusion because the dissolved substances tend to distribute themselves evenly throughout the available pore space. Although the internal transport of fluids within the pore spaces of the sediment is small, over geologic time it can be quite substantial. The rate of flow is dependent upon both permeability and grain-size of the sediment and reactions will occur through the mixing of introduced fluids with connate water. Changes in pressure, temperature, and composition of the dissolved matter can lead to precipitation of dissolved minerals. It is by this process that voids are filled, for example, inside the camerae of ammonites and nautiloids that have not been infilled by sediment and in which drusy calcite or quartz may develop (Fig. 38).

As grain size changes, solubility increases and large grains continue to grow at the expense of smaller ones that are being dissolved. Void spaces are occluded as minerals are precipitated within them. Organic materials are altered or destroyed. In addition, metasomatic processes commonly occur. Similarly, unstable polymorph substances are changed to their more stable forms. If fossils in sedimentary rocks are exposed to weathering, the equilibrium reached during diagenesis is disturbed. Among processes responsible for such changes are hydrolysis, hydration, oxidation, and reduction, and attacks by acid or alkaline solutions. If temperature and pressure are sufficiently increased, diagenetic processes change to metamorphic processes, leading to extensive changes in mineralogy and texture of the rock (WINKLER, 1964). As stated before, there is no well-defined dividing line between the two processes. Fossils are known to be preserved in regions of contact and regional metamorphism, and can play an important role in the interpretation of such metamorphic strata (BUCHER, 1953; RINEHART *et al.*, 1959).

Of the many diagenetic processes, a few are discussed below because they are important for accurate interpretation and understanding of fossils.

FORMATION OF STEINKERNS AND EARLY DIAGENESIS

The body of an organism can be completely preserved as a body fossil. If it is destroyed within the sediment, and if the sediment is sufficiently lithified, and no secondary minerals are being precipitated, a void is created that may be preserved as such. The inner surface of the void is an impression of the outside of the destroyed object.

Solution of, for example, bivalve shells and subsequent filling of such voids by drusy formations, such as calcite, dolomite, or siderite, is relatively rare (BATHURST, 1967).

If the sediment is not sufficiently competent to maintain these voids, they may collapse; however, if the shells initially possess an internal void or if such voids are created during early diagnesis by removal or decomposition of soft parts, they are commonly filled by sediment. It is by this process that true steinkerns develop that reflect the internal morphology of the shell (Fig. 39).

Steinkerns are produced by many types of sedimentary infilling and have an amazing variety of shapes and textures. Frequently they undergo internal sedimentation and develop geopetal structures. Commonly, smaller fossils and burrows are found in them (Fig. 40). Study of steinkerns allows important conclusions to be drawn with regard to the life habits of an individual organism and the particular conditions of sedimentation. For example, calcilutite and pelletal limestones can occur next to marly limestones and shell debris deposits.

FIG. 38. Medial section through the phragmacone of the ammonite, *Ceratites,* in which the walls of the camera are lined with transparent drusy calcite. Middle Triassic (upper Muschelkalk, middle Ceratites Schichten), Thuringia; ×2.5 (Müller & Zimmermann, 1962).

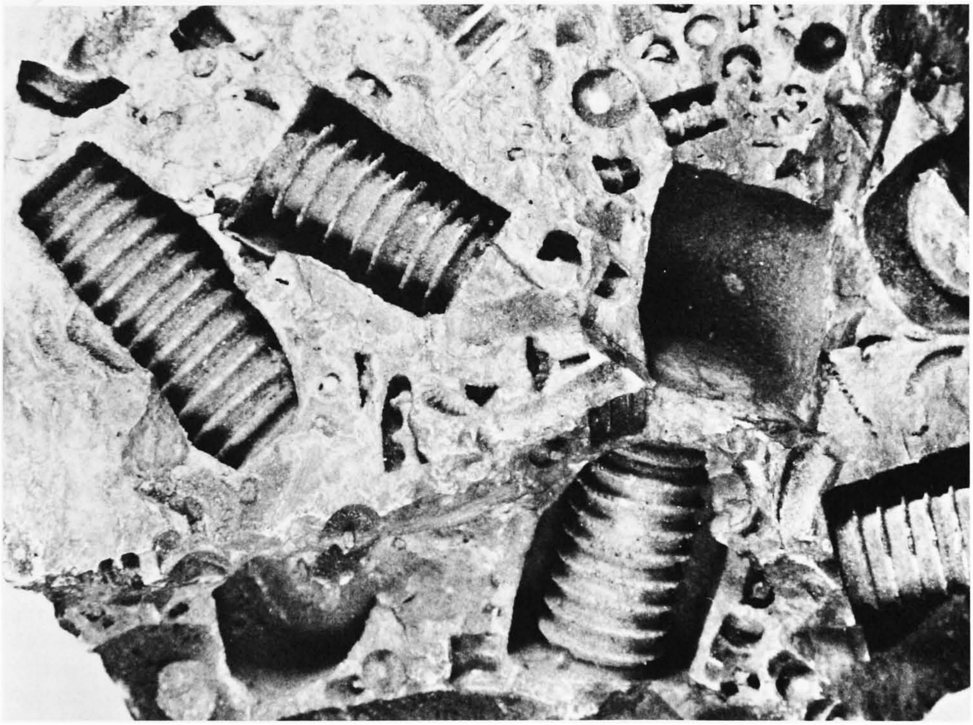


FIG. 39. Fragments of crinoid columnals (*Ctenocrinus typus* BRONN). The lumen filled with sediment, prior to dissolution of the columnal, producing a true steinkern which reflects the soft part morphology of the animal. Lower Devonian (Spiriferensandstein), Eifel, West Germany, approx. ×2.75 (Müller, 1963).

Multiple phases of fine-grained sedimentation can occur within shells by recurrent water movement. Material in suspension then settles within the shell, especially if the currents flowing out of the shell are weak. In planispiral ammonite shells that are being filled with sediment through their apertures, the sediment in the camerae becomes increasingly finer and more homogeneous toward the apical end. Many camerae receive no sediment and remain empty and most shells are not entirely filled. In order to become completely filled, a hole at the apical end of the shell would have to exist (SEILACHER, 1968a).

When shell substance is gradually destroyed, the surrounding sediment may settle slightly, and the steinkern may be pressed against the impression made by the outer surface of the shell, so that this is then imprinted on the steinkern. Such structures are called *Prägekerne* or *Skulptursteinkerne*. Their analysis helps in the interpretation of early diagenetic processes in the surrounding sediment as well as the manner of dissolution and decomposition of the organism itself. Sculptured steinkerns are most frequently formed as the result of the destruction of organisms with calcareous hardparts, in particular, bivalves.

The dissolution of shell material can begin on either the interior or exterior surface of the shell. Dissolution has been shown to be extremely strong in fractured shell material. The synchronous dissolution of shell material can also lead to the decrease in shell thickness and the loss of sculpture. Shells are most easily reduced in thickness at the umbonal region where they were originally the thickest. This type of shell destruction is mostly the result of processes occurring outside the sediment, prior to burial. In both these cases of shell reduction, it is thought that the conchiolin and the periostracum are destroyed. In oxygen-rich environments, the periostracum is generally

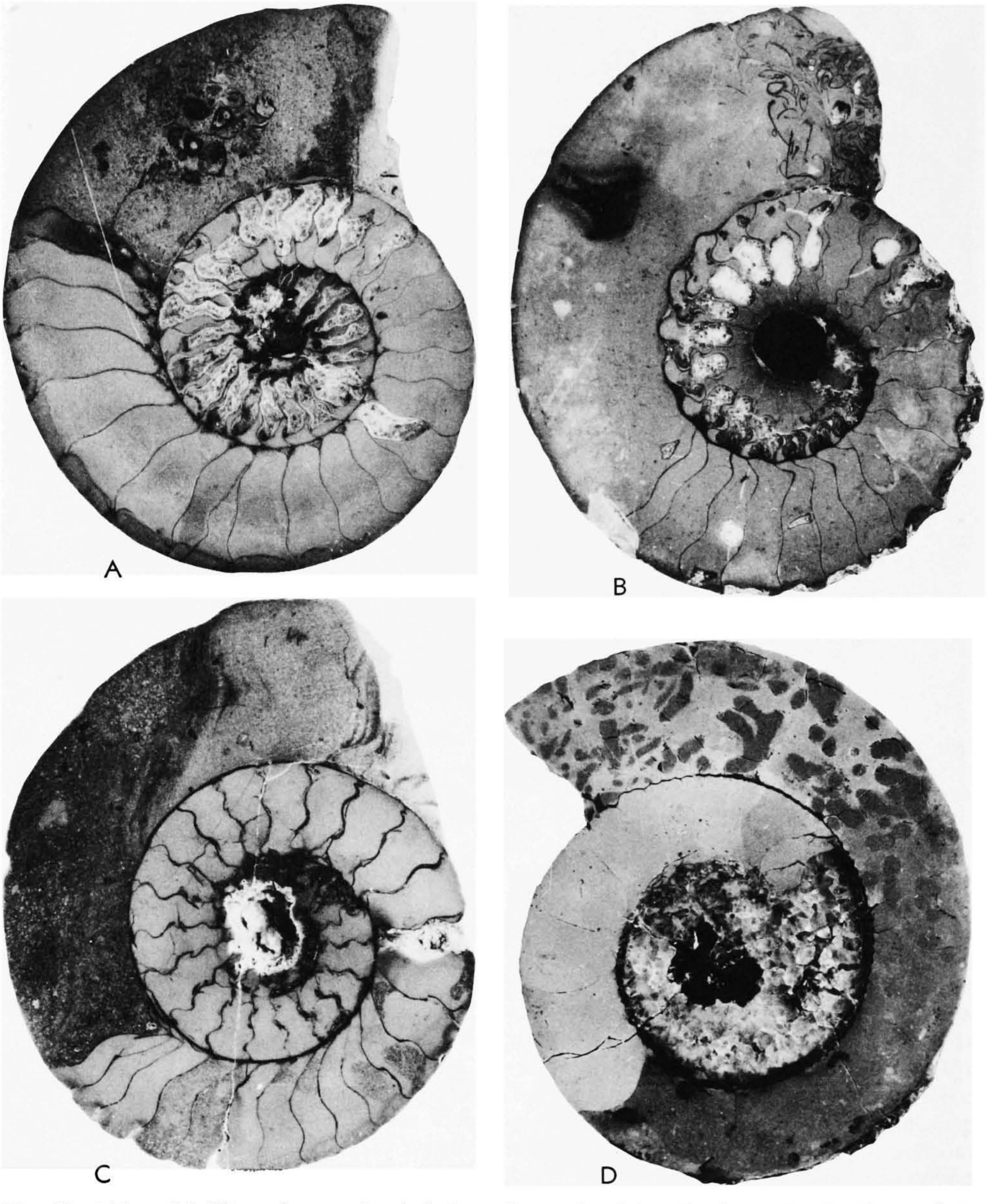


FIG. 40. Differential filling of ammonite shells by sediment (medial sections).——*A. Ceratites evolutus* PHILIPPI, upper Muschelkalk (*C. evolutus* Zone), Ohrdraf, Thuringia; diameter 95 mm.——*B. Ceratites evolutus* PHILIPPI, upper Muschelkalk (*C. evolutus* Zone), Ballenstedt, Harz Mt.; diameter 100 mm.——*C. Ceratites* cf. *C. compressus* PHILIPPI, upper Muschelkalk (*C. compressus* Zone), Remda, Thuringia; diameter 85 mm.——*D. "Perisphinctes"* sp., lower Malm (Oxfordian), Staffelstein, Franconia; diameter 65 mm (Sektion Geowissenschaften, Bergakademie Freiberg, 249/3-6; Müller, n).

destroyed first; the inorganic constituents remain. In oxygen-deficient environments, especially those with high concentrations of hydrogen sulfide, destruction begins with the dissolution of calcareous components. The oxidation of sulfides frees sulfuric acid, which dissolves calcareous material and hinders additional bacterial destruction of organic substances, as decay-producing bacteria are extremely sensitive to the presence of oxygen.

In anaerobic environments, the periostracum protects the underlying shell material, but there is a considerable difference in the solubility of the prismatic and the nacreous layers. The prismatic layer of the shell, secreted by the mantle edge, is generally calcite, whereas the nacreous or porcellaneous layer of the shell consists of more soluble aragonite, which is secreted by the mantle surface. The shells of snails and dimyarian bivalves, whose shells are composed entirely or predominantly of aragonite, are therefore most commonly preserved as steinkerns. The shells of monomyarians are predominantly of calcite and their shells are generally preserved in their entirety.

If the voids created by solution of skeletal material are preserved, solution must have occurred after lithification of the sediment. Occurrences of sculptured steinkerns show that the solution of the shells proceeded outward from the inner side. They can only be formed if the sediment has not become entirely lithified, when the void can be closed under the weight of the settling sediment. During this process, the steinkern moves outward with the progressive solution of the inner side of the shell. Imprinting of the outer ornamentation on the steinkern occurs only after the shell substance has been completely removed.

Sculptured steinkerns of ammonites are known from the *Posidonia Shale* (Lias ε) and the Solnhofen Limestone in southern Germany. They show details of ornamentation without preservation of sutures.

Aragonite can be replaced in skeletal material by the action of marine boring algae, and probably fungi and bacteria. Algal filaments penetrate the shell material centripetally and eventually die and decompose. The resulting cavities can be filled with micritic cements. When this process is repeated, as has been observed in mollusk shells from the Bahamas, a micrite envelope or rind will develop around the shell, which for unknown reasons is not dissolved during diagenesis. Thus, an impression of the original shell is preserved, which later may be filled with calcite crystals (Bathurst, 1966; Wolf, 1965).

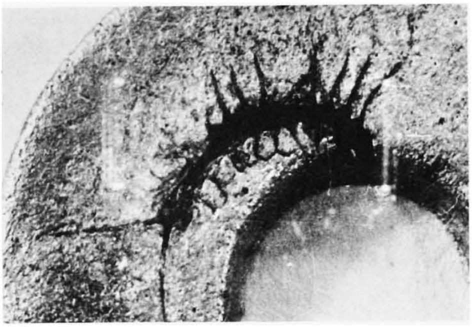


Fig. 41. "Metallofact," casting of recent myriapod in molten aluminum, ×1 (Müller, 1963).

Fossils can also be preserved in lava flows. For example, tree trunks which were surrounded by lava can leave many details of the bark clearly imprinted in the surrounding rock, and in some cases, the cell structure of trees has been preserved ("lava trees"). Even a rhinoceros has been preserved in basalt (Chappell *et al.*, 1951). Of particular interest, is the "metallofact" shown in Figure 41, which is a myriapod that was rapidly covered by molten aluminum, thereby preserving its shape.

DEFORMATION OF FOSSILS

GENERAL DISCUSSION

Fossils are commonly found to be deformed by mechanisms that either deform them plastically or fracture them. Of course there are many transitional cases between these two end results. Possible causes for such deformations are: 1) volume decrease of surrounding sediment, 2) collapse due to overburden, and 3) tectonic movements.

VOLUME DECREASE (SETTLING) OF SEDIMENT AND ITS EFFECTS

GENERAL DISCUSSION

Settling of sediments may be caused by the following processes: 1) reduction of interstitial liquid (mostly water), 2) leaching of relatively soluble constituents, and 3) removal of organic matter by degassing. Compacting of sediments can occur during sedimentation under the influence of outside factors such as water movement. As a consequence, pore volume is reduced. Since the wettability of coarse-grained sands

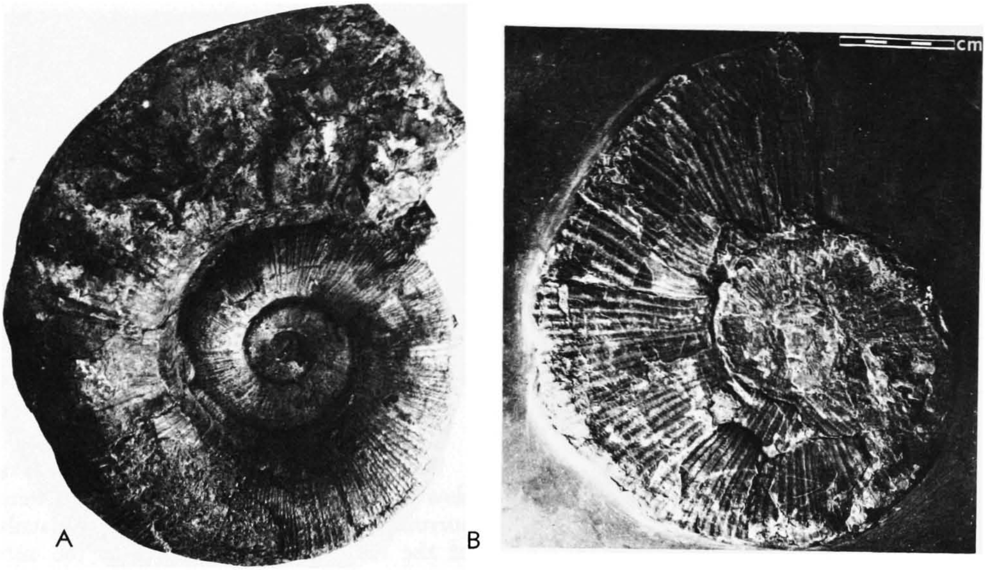


FIG. 42. *Lytoceras* sp.——*A*. Preservation in limestone (Lias α, Braunschweig).——*B*. Specimen deformed by compaction and dewatering of clay-rich sediments (Lias ε, Posidonienschiefer), southern Germany. Shell walls are fractured and laterally displaced during sediment compaction. Scale in cm (Müller, 1963).

is small, maximum compaction may result at this stage. Thus, sands deposited under turbulent conditions, as a rule, will not suffer further compaction, except when they contain a significant amount of organic substances, or easily soluble components, or hollow fossil remains. But even in such conditions, deformation of fossils will occur only occasionally, because hydrostatic pressure is reduced by the friction and mutual support of sand grains.

One can think of porous sand as being composed of numerous, vertical prisms, with their sides in contact, along which downward movement takes place. Since the cross sections of these prisms are relatively large, only fairly large-sized objects can be deformed. Most objects that have relatively small cross sections remain undeformed in such sands. However, deformations due to the weight of the object itself are in a different category. They can occur, if organic tissues are decomposed and yield.

What is true for sand deposits is not necessarily valid for boulder beds. As do single grains in sandstone, pebbles and boulders in conglomerates can support each other to form arches. Little or no deformation should, therefore, be expected, just as in sands; however, the opposite appears to be the case. The reason for this can be found in stress changes that develop, as in sand, when, under load pressure, edges and corners of grains break off. This happens most commonly if the interstices are not entirely filled with sand or some other material.

Porous sediments, which are very fine grained or are composed of colloidal constituents, have considerable water retention because of their large internal surfaces. This is especially true when clay minerals of the montmorillinite group compose a large portion of the sediment. Also, clay commonly contains large amounts of organic material and is, therefore, subject to more settling than other types of sediments (Fig. 42,*B*).

The settling of clayey sediment is caused by increasing sediment accumulation and load pressure, which results in dewatering of the clay particles. During dewatering, the migration of pore fluids out of the sediments not only causes a reduction in volume but also the migration of dissolved substances, which are deposited elsewhere. In this way concretions can be formed, which may be of limonite, phosphorite, marcasite, pyrite, barite, or calcium carbonate (ILLIES, 1950).

During dewatering, lime mud may lose as much as three-fifths of its volume and one might, therefore, expect to find considerable settling effects in such sediments; however, fossils preserved in pure limestone, free from clay particles, silica, or organic material, generally show few signs of early diagenetic deformation (Fig. 42,*A*). This is probably because dewatering and solidification of very stable carbonate mud take place at a very early stage, and the concomitant volume and stress changes do not affect the texture of the rock and its contained fossils. In contrast to clayey and marly sediments, calcareous muds are not subject to later volume reduction by compaction (MÜLLER, 1951a). They pass rapidly through the plastic state, before the deposition of a large amount of overlying sediments. As soon as such sediments have been lithified, no further diagenetic deformation can take place.

The deformation of ammonites with rounded shells and wide living chambers, such as *Ceratites nodosus*, depends upon their mode of embedding. If the shell is oriented parallel to the bedding, it is generally flattened. Shells that are embedded vertical or oblique to the bedding are broadened. Oblique deformation can sometimes be mistaken for tectonic deformation of the shells. Therefore, taxonomic identifications can become more difficult because the cross section of the whorls may be changed during deformation. The diameters of vertically embedded ceratites can be shortened by as much as 30 percent, with little indication of such compaction in the surrounding rock.

If outlines and cross sections of undeformed fossils are well known, the study of deformed specimens may lead to conclusions about the degree and cause of diagenetic deformation. If forms are not known in their undeformed state, then accurate analyses cannot be made and misidentifications may result. This has undoubtedly led to the establishment of many unnecessary species in the literature, especially when many of these fossils have undergone plastic deformation (REGINEK, 1917).

FIG. 43. *Psiloceras (Caloceras) johnstoni* (SOWERBY), showing early diagenetic deformation; from Lower Liassic (αlb, lower Hettangian), Göttingen, West Germany. Largest diameter, 95 mm (Langheinrich, 1966).

PLASTIC DEFORMATION

If an object does not possess some original elasticity, plastic deformation can only occur after diagenetic decomposition and leaching have made it pliable. In general, plastic deformation of steinkerns occurs only when the hard parts have been dissolved prior to lithification of the surrounding sediment. In lower Liassic rocks (αlb, lower Hettangian) of Göttingen, the ammonite shells are "stretched out" along bedding planes, having been deformed during early diagenesis (Fig. 43) (LANGHEINRICH, 1966). In this example, the amount of deformation (as determined by comparing long and short axis of a deformation ellipse) is 84 percent. There is no evidence of tectonism in these deposits, and, therefore, deformation must have occurred during early diagenesis. Thus, all observations concerning decalcification of hard parts due to decomposition of organic substances in or on unconsolidated sediments are of considerable importance in order to understand the process of plastic deformation. This type of deformation occurs primarily in sediments with a high clayey content, and practically not at all in sandstone and pure limestone.

The amount of decaying material must be somewhat substantial. HECHT (1933) studied experimentally the effects of skeletal material during the decay process. He added a number of *Mytilus* valves of known

TABLE 5. *Solution of Bivalve Shells in a Medium of Decaying Soft Parts (after Hecht, 1933).*

Time in Days	Original Weight (grams)	Subsequent Weight (grams)	Weight Lost (grams)	Percent Loss
7	0.8471	0.7205	0.1266	14.9
14	0.8471	0.6204	0.2167	24.5
16	1.5603	1.3870	0.1733	11.1
16	1.8466	1.3870	0.4590	24.86
31	1.6628	1.4650	0.1978	11.86
32	1.6628	1.4824	0.1804	10.85

weight to the flesh of 100 specimens of the same species. At intervals the shells were weighed to determine the amount of calcareous material lost due to the action of acids produced during decay. The results are shown in Table 5. In general, the greater the content of organic material within the sediment, the greater the possibility for the dissolution of calcareous shell material. The most important chemical agent seems to be the carbon dioxide produced during decay in addition to sulfuric acid, which is the oxidation product of hydrogen sulfide normally present in the sediment.

FIG. 44. Wrinkled but undestroyed periostracum of *Inoceramus dubius* from Upper Liassic (Lias ε, lower Toarcian, Posidonienschiefer), Goslar, Harz Mt., ×0.93 (Müller, 1963).

Because the periostracum protects the outer shell layer from solution, the unprotected, internal layers are relatively rapidly dissolved, and thin shells may be reduced to a chalky substance within a few weeks. In thicker shells the periostracum, which consists of conchiolin, begins to peel off after eight weeks without having undergone any changes. It is thrown into folds, parallel to the growth lines, and can be easily detached. In addition to bivalve shells (Fig. 44), arthropod carapaces are sometimes found having such wrinkled surfaces. If the shell or cuticle are not completely dissolved, but have become flexible, impressions of foreign objects or other parts of the same organism are occasionally found on the periostracum.

Hard parts that have become soft and flexible under the influence of organic decomposition products are easily subject to plastic deformation. If the rocks containing them have not been tectonically deformed, their occurrence always indicates that solution has been at work. As an example, fossilized skeletons can be found with individual bones bent and superimposed upon each other on a single bedding plane. In such cases the bones were made soft by diagenetic processes prior to compaction of the sediment. Examples are found among the reptilian remains in the *Posidonia* Shale near Boll and Holzmaden (Württemberg).

DEFORMATION BY FRACTURE

Deformation by fracture can occur if 1) the object has insufficient primary elasticity, and 2) an originally elastic body has become brittle by decomposition and leaching processes.

If during compression of the sediment, a shell cannot expand laterally, then it may break under pressure, and the individual shell fragments are thrust over each other.

The cracks that are formed during fracture deformation of shell material are usually delicate. If the broken fragments suffer no displacement and if they are recemented by mineral precipitation, plastic deformation may be simulated, and imprints of the cracks may be seen on steinkerns. Such specimens show clearly that fracturing preceded solution.

An example of fracturing deformation is shown in Figure 45,*A-C*. If a shell has essentially a circular outline, it is possible to divide the fracture systems into two basic types: 1) concentric fractures, running parallel to the shell outline, and 2) radial fractures that originate from the center of the shell.

Shells with oblong, oval outlines such as the bivalves *Mytilus*, *Modiola*, and *Inoceramus* (Fig. 45,*C*), display characteristic fracture. Commonly a main fracture line runs along the central crest of the shell (Fig. 45,*B*). Objects usually break up along cracks that are oriented at right angles to their sides.

Experimentally, individual shells of bivalve mollusks and brachiopods are capable (according to species) of supporting normal loads of 500-4,000 kg/m^2 before breaking. Natural examples of shell packings could therefore support without collapsing a sedimentary overburden comparable in thickness to one meter. Thus, there may be ample time for cementation to begin, and further strengthen the packings, before critical overburden thicknesses are reached (ALLEN, 1974). Pressure mechanics have recently been applied to the study of skeletal hard parts by BRENNER and EINSELE (1976).

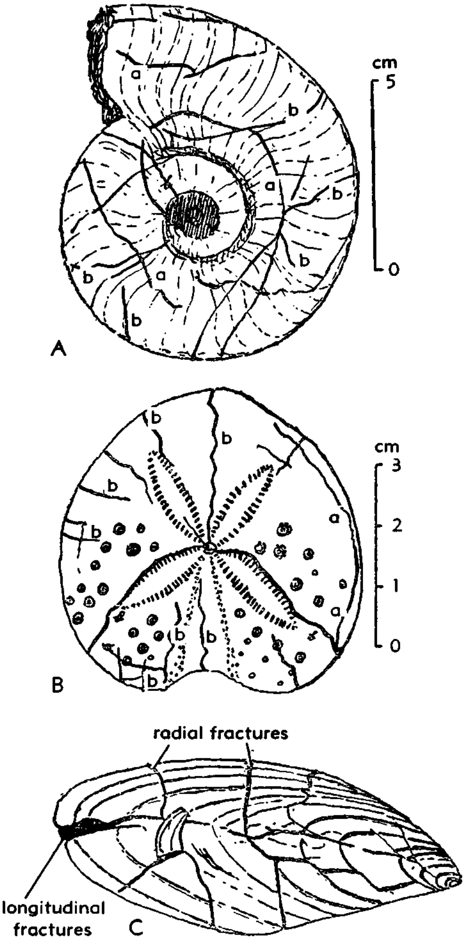


FIG. 45. Types of deformation by fracture of fossils with rounded outlines (*a*, concentric fracture; *b*, radial fracture) (Müller, 1951b).——*A. Leioceras opalinum* REIN., lower Dogger, Goslar.——*B. Echinospatagus hofmanni* GOLDFUSS, upper Oligocene, Bünde near Herford.——*C. Inoceramus labiatus* VON SCHLOTHEIM, lower Turonian, Salzgitter.

In some cases the result of sedimentary pressure can also be recognized in the absence of shell deformation. This is common in bivalves preserved with articulated valves where one valve is pushed over the other. This is especially common in isodonts and desmodonts such as *Pleuromya, Mya,* and *Gresslya*. Without contemporaneous deformation of the valves, this position is observed when compaction of the sediment has led only to a shifting of the shells, not to fracturing or plastic deformation. It is not observed in clayey deposits and is restricted to limestone and calcareous marl, for example, the Ceratite beds of the upper Muschelkalk.

COLLAPSE UNDER OWN WEIGHT

If a shell collapses under its own weight, the degree of deformation is determined by its inherent statics and mechanics. Plastic deformation commonly occurs: 1) in elastic

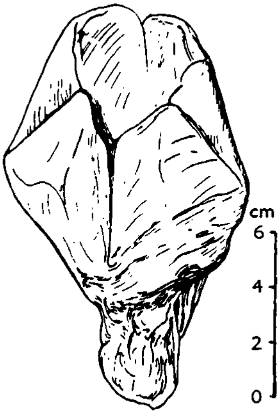


Fig. 46. *Conularia tulipa* Richter & Richter crumpled like a paper bag by pressure. Lower Devonian (Bundenbacher Schiefer), Bundenbach, Rhineland (Richter, 1931).

forms, especially thin-walled shells (Fig. 46), and 2) in shells that have become flexible as a result of the processes of decomposition and leaching.

On the other hand, deformation by fracture is to be expected if hard parts become brittle during decomposition or leaching.

DEFORMATION BY TECTONIC STRESS

Tectonic movements, especially during periods of intense orogeny, can result in considerable deformation of fossils. However, whereas pressure exerted during settling of unconsolidated sediment acts perpendicular to the bedding planes, causing changes in both the shape and volume of shells, tectonic pressure may act in any direction and generally leads to changes in shape and not volume. It is generally quite easy at the outcrop to tell the two types of deformation apart; however, in unoriented hand specimens this may prove difficult. Just as in pelomorphic deformation, tectonic deformation may result in a variety of forms that can simulate a variety of species depending on the original position of the fossils in the rock. Thus, it could be shown, in some cases, that several hundred "new" species were proposed without taxonomic justification (Reginek, 1917; Fanck, 1929; Breddin, 1964). This is true for mollusks, and for other organisms, such as graptolites. So many types of deformation can result in these deposits, that mistakes are inevitable (Fig. 47,*A-F*).

A distorted fossil can be restored accurately if the degree of deformation, δ, is known. "δ" is the ratio between the long and the short axes of the deformation ellipse within a given bedding plane, and frequently, it is only a minimum number if the fossils are less easily deformed than the surrounding rock. In the case of steinkerns and molds, both are composed of the same material as the surrounding rock, and they therefore become deformed to the same degree as the rock.

Original right angles in fossils (e.g., between hinge and median lines in some ribbed bivalves and brachiopods; between axis and posterior margin of cephalon and thoracic segments in trilobites) may be deformed into oblique angles which then correspond to the conjugate diameters of the deformation ellipse. If two such oblique angles can be measured for two fossils lying in the same bedding plane, the deformation elipse can be transformed into a circle and the degree of deformation can be determined (Fig. 48,*A,B*). Langheinrich (1968) has published a review of the several methods by which the deformation degree δ in a particular bedding plane may be determined from changes of angles.

If the degree of deformation is known, it is possible to use different methods of restoration of the fossils. Such techniques have been described by Gräf (1958), Baumann (1958), de Vries (1959), Sdzuy (1962), Breddin (1964), Stehn (1968), and others.

SELECTIVE DISSOLUTION DURING DIAGENESIS

Skeletal material exposed at the water-sediment interface is unstable and is selec-

Fig. 47. Tectonic deformation of graptolites, Lower Silurian (Valentian), Weinbergbruch (vineyard quarry) near Hohenleuben (eastern Thuringia); direction of deformation (*b*-axis) for *A-C* marked by double arrow (Schauer, 1971).——*A-D. Monograptus turriculatus* Barrande; *A,* tectonic "long form" (deformation parallel to *b*-axis); *B,* tectonic "inclined form"; *C,* tectonic "short form," deformation

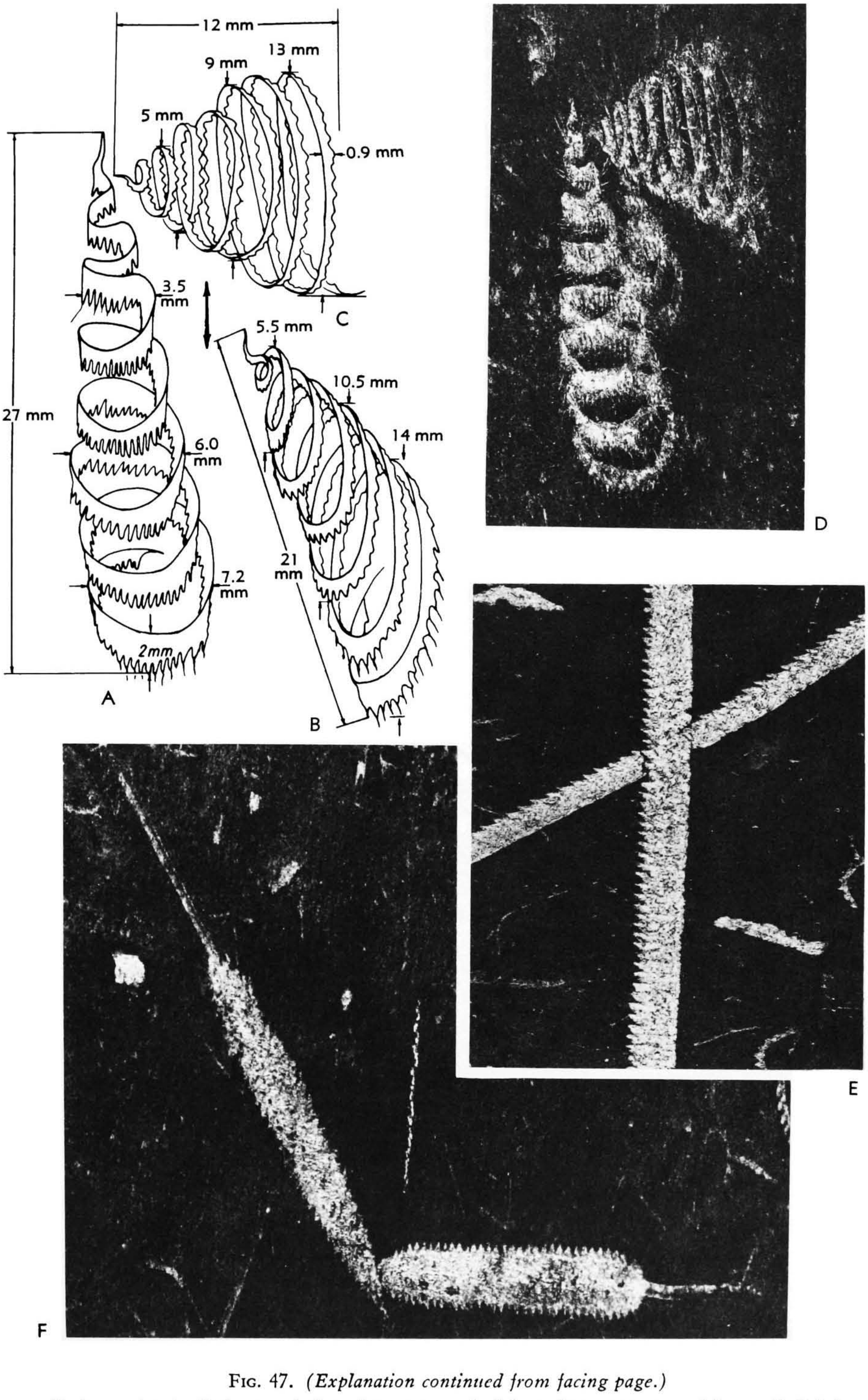


FIG. 47. *(Explanation continued from facing page.)*
perpendicular to *b*-axis; *D,* long and short form on one bedding plane, approx. ×1.9.——*E, Pristiograptus nudus nudus* LAPWORTH, approx. ×1.9.——*F. Petalograptus altissimus* ELLES & WOOD, approx. ×1.3.

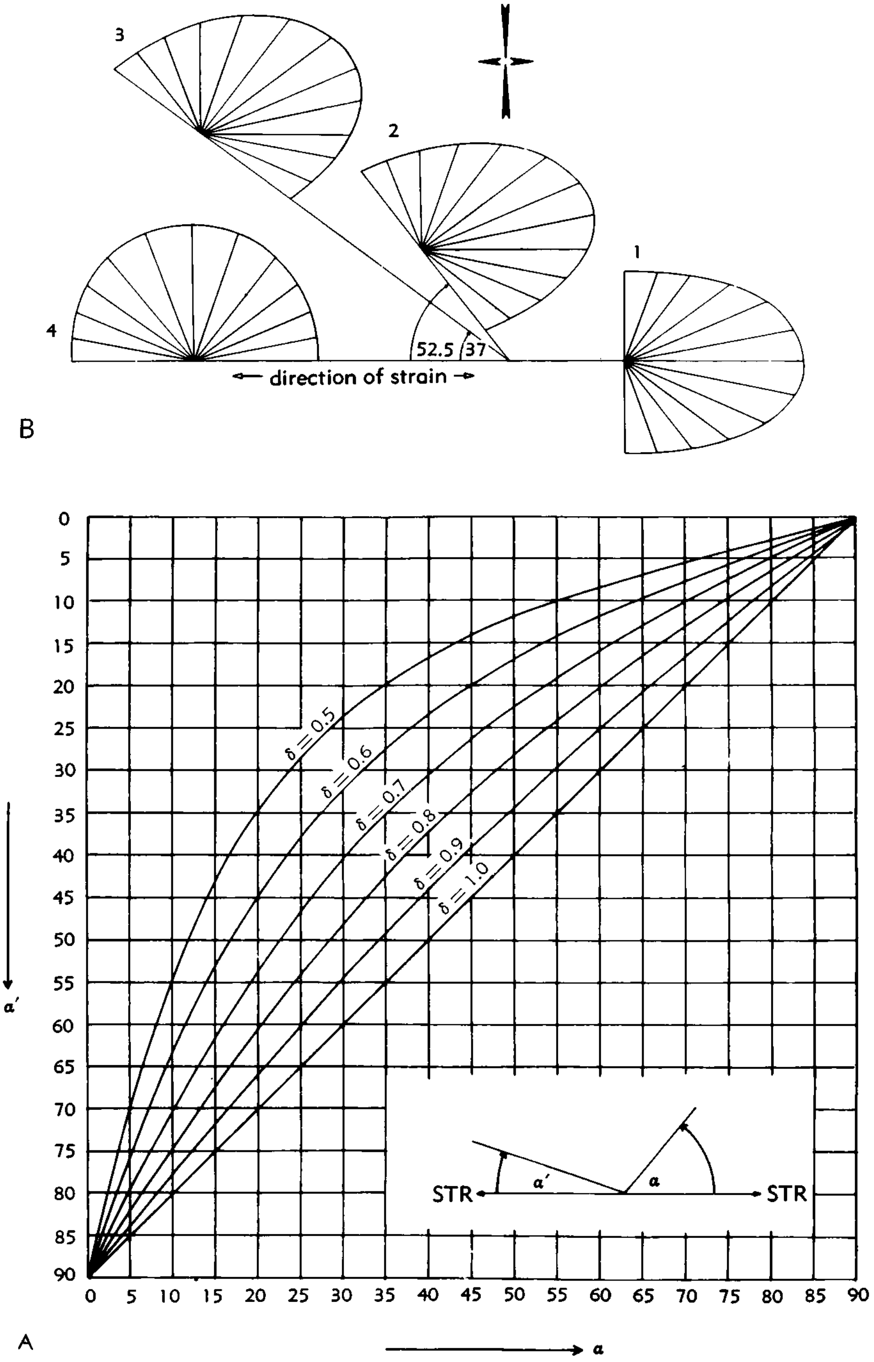


FIG. 48.——*A*. Graphic representation for determination of δ. α and α′ indicate the angle between the direction of elongation *(STR)* and the two lines, respectively, within the fossil, which formed a right angle before deformation (Mädler, 1938).——*B*. Four deformed bivalves (δ = 0.75) having original width-length ratio of 1.36, with their shell margins oriented at different angles *(α)* to the direction of

tively dissolved according to the solubility of its component substances. This process has been studied in recent and fossil material and much of the work has been substantiated by studies in phase chemistry. Lowenstam (1963) summarized the mineralogy of skeletal materials.

It must be remembered that the solubility, and thus preservability, of skeletal elements are influenced by the microstructure of their elements and the content of easily destroyed organic matter such as is found between the prisms in the shells of clams (Kessel, 1938).

Selective solution of skeletal material also occurs during diagenesis, mainly under load pressure, by an upward migration of pore fluids caused by the pressure of accumulating sediment. By this process a "solubility front" develops, especially in the transition between oxidation and reduction zones, under conditions of low pH (Jarke, 1961). Under anaerobic conditions, hydrogen sulfide can have the same effect on skeletal material as carbon dioxide in sea water. Therefore, hydrogen sulfide need not be oxidized to form sulfuric acid. This explains absence of gypsum, which otherwise would be expected to form during dissolution of calcareous skeletal material (Mosebach, 1952).

In the bituminous *Posidonia* Shale (Lias ε) of southern Germany, the aragonitic portions of ammonites have been dissolved, but the calcitic aptychi, the siphuncles, and the periostraca are preserved. Selective dissolution can also occur under aerobic conditions as can be seen in the Solnhofen Limestone (Malm Z, lower Portlandian) in southern Germany, where aragonitic shells of ammonites have been entirely destroyed. As a rule, only faint outlines of the shells remain; however, the aptychi and siphuncles are well preserved.

The speed at which shell material is dissolved depends on the effective surface area. Thin shells may be completely dissolved when remnants of thicker shells are still present. Phosphatic and horny skeletal elements (such as brachiopod shells, gastropod opercula, hooks of coleoids, scolecodonts, arthropods, graptolites, bones, teeth, and scales of vertebrates) may be preserved in acidic environments in which calcareous hard parts are completely destroyed.

MOLECULAR REARRANGEMENTS IN THE COURSE OF DIAGENESIS

GENERAL DISCUSSION

Molecular rearrangements occur during diagenesis when, under the influence of temperature and pressure, existing imbalances are corrected and individual sedimentary particles attain a state of minimal surface energy. Several possibilities exist of which the following are important: 1) recrystallization, especially grain growth, aggrading neomorphism; 2) concentration of thinly disseminated substances with or without chemical reactions (metasomatism); and 3) transformation of substances from unstable into more stable forms.

RECRYSTALLIZATION IN PARTICULAR GRAIN GROWTH

Recrystallization occurs within the sediment, in regions of pore water movement, and is controlled by solubility, grain size, and temperature. During this process, organic hard parts incorporated in the sedimentary matrix are also recrystallized. Such diagenetic changes usually result in changes in grain size, form, and orientation of particular mineral species and their polymorphs (Folk, 1965). Commonly, the process is characterized by the increase in size of larger grains at the expense of smaller ones. Because the ratio of surface to volume is less in large crystals than in smaller ones, an upper limit of grain growth exists under any given set of circumstances. Organic hard parts can be so intensively recrystallized by grain growth that they are often unrecognizable, except for a thin "dusk line" which represents the shell margin (Folk, 1965).

(Continued from facing page.)

elongation. The angles (α) of 0, 37, 52.5, and 90 degrees correspond to deformation of 0, 45, 60, and 90 degrees, respectively, corresponding to shells numbered 4, 3, 2, and 1 (Langheinrich, 1968).

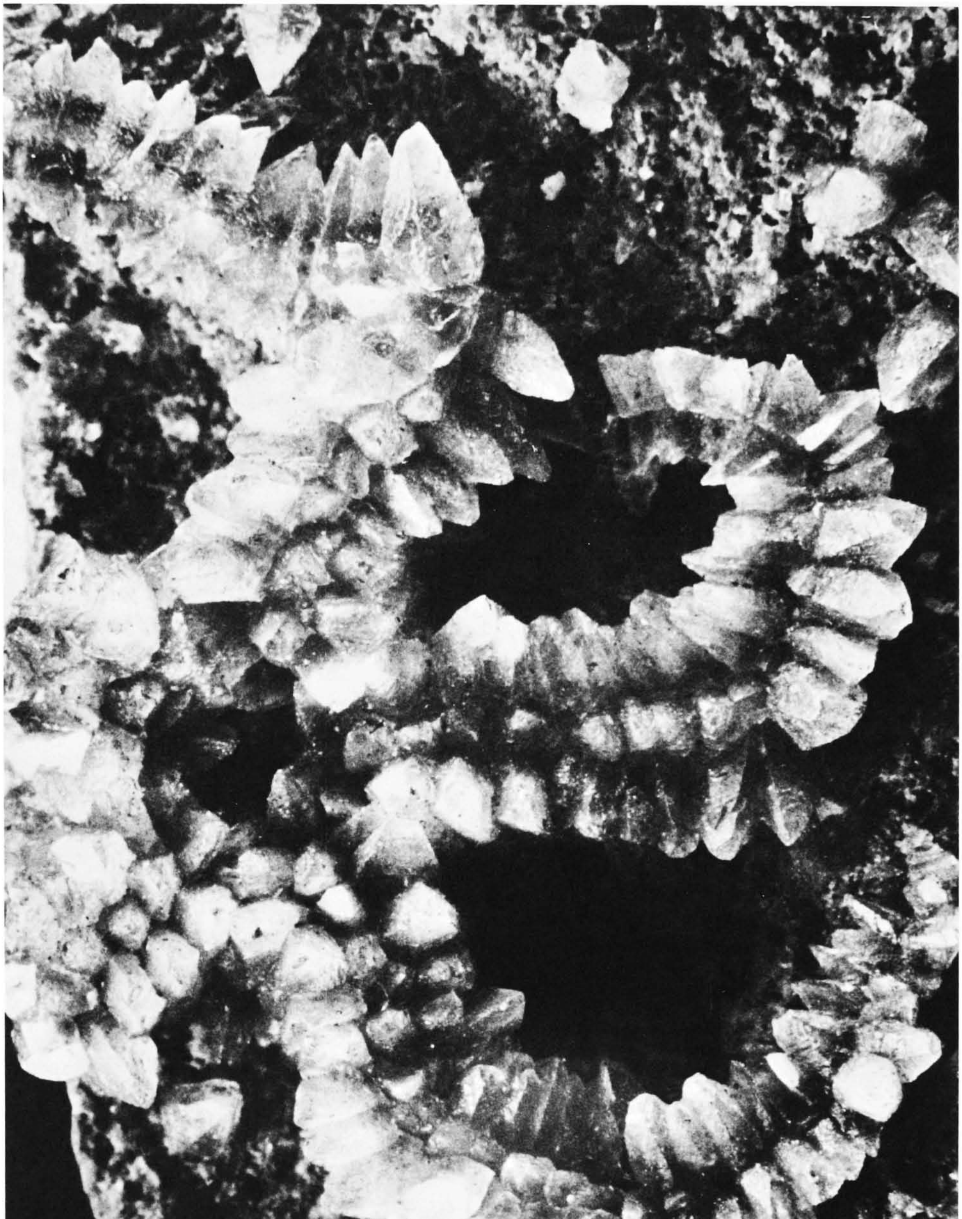


FIG. 49. *Aspidura* sp., in space not completely filled with sediment underneath a convex-up bivalve shell; the dorsal plates of the ophiuroid carry large, sparry calcite crystals. Middle Triassic (upper Muschelkalk), Württemberg; width approx. 30 mm (Müller & Zimmermann, 1962).

Small, fragile organisms, consisting of calcareous material, are commonly destroyed during the initial stages of diagenesis. Coccoliths are especially susceptible to complete recrystallization, either by load pressure or shearing stress, and quickly lose their characteristic shape. During the diagenetic alteration of a marl into a marly limestone, coccoliths can become encrusted with slowly growing crystals to such an extent that they are no longer recognizable. As a general rule, the older the sediment, the less likely the chance of finding identifiable coccoliths. Recrystallization of shell material can also result, without appreciable accompanying grain growth, in the solid state through solutions, depending on the porosity and permeability of the rocks (FÜCHTBAUER & GOLDSCHMIDT, 1964, p. 195). During such processes primary textures are generally preserved, because the changes generally take place within crystal lattices (BATHURST, 1958).

If recrystallization is very extensive, it leads to the development of a coarsely crystalline mosaic texture and the complete obliteration of original, internal structure. This can commonly occur during the inversion of aragonite to low Mg-calcite or during aggrading neomorphism of small calcite crystals. Such textures are not only found in fossils, but also in the matrix of carbonate rocks where sharp boundaries exist between matrix and shells (HOLLMANN, 1968a).

Processes of recrystallization and grain growth aid in the natural weathering of fossils when they can be easily separated from the sedimentary matrix by chisel or acid. Bivalve shells and echinoderm plates are naturally quite sturdy, but diagenetic changes may increase their durability. Because the rate of weathering is dependent upon grain size, durable shells weather at a much slower rate than matrix of similar mineral composition. The motion of pore fluids is particularly important in the transporting and removal of constituents. Fluids preferentially move along crystal boundaries, and with special intensity along boundaries between shells and matrix, where small cavities eventually develop around the shells, facilitating their removal from the rock.

It is sometimes possible to determine the length of time during which recrystallization took place if the fossils suffered fracturing during diagenesis. It must be remembered, however, that fissures caused by early diagenetic settling may be closed by later recrystallization.

Echinoderm tests are especially susceptible to recrystallization. Each plate is composed of a meshlike, porous skeleton of a calcite crystal whose crystallographic orientation is determined by the structure of the animal's body (MACURDA & MEYER, 1975). During early diagenesis, these pores are filled by optically continuous calcite cement, until each skeletal element forms a single calcite crystal with characteristic cleavage. If space is available, epitaxial overgrowths commonly form around the plates and assume scalenohedral shapes. This process can severely alter the appearance of an echinoderm, and new species have been introduced for diagenetically altered specimens.

Hollow echinoid tests, such as occasionally seen in chalk, are formed through oriented growth of the plates, each of which has a calcite crystal growing on the inside; all the crystals keep growing until the inner lumen is filled. The same explanation can also be applied to the so-called "crystal apples" where calcite crystals have completely filled the inside of the test of *Echinosphaerites*. Echinoderm tests can also change their appearances by outward growth of calcite crystals. Figure 49 shows a specimen of *Aspidura* from the Muschelkalk in which the dorsal plates bear calcite scalenohedra (MÜLLER, 1969a).

An especially interesting phenomenon occurs when repeated precipitation of silica takes place in the interior of an echinoid test. In the specimen shown in Figure 50, the test of an echinoid was first filled to a certain level by chalky sediment, which was changed metasomatically to chert. Later, calcite crystals grew inward from the plates, until the remaining void was filled with light-colored, rather coarse-grained quartz. Finally, the remains of the calcareous skeleton were dissolved (Fig. 51).

Thin sections of limestone samples, for example, red limestones of the Oxfordian, Kimmeridgian, and Portlandian show Fora-

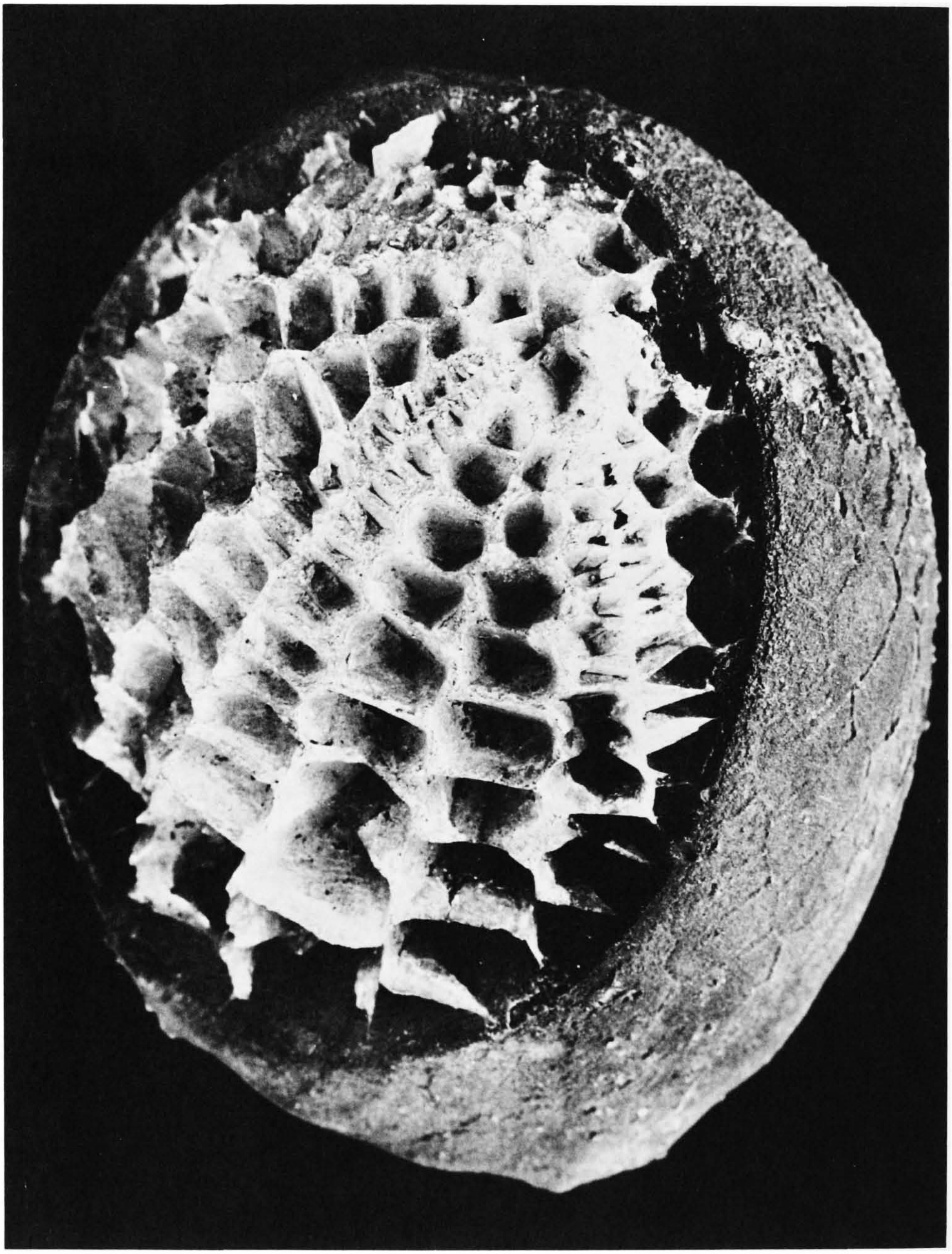


FIG. 50. *Echinocorys* sp.; internal structure is due to repeated precipitation of silicic acid (compare with Fig. 51). Upper Cretaceous (lower Maastrichtian, chalk facies), Rügen, DDR; largest diameter, 80 mm (Müller & Zimmermann, 1962).

minifera and other microfossils whose shells have been altered by calcite overgrowths (HOLLMANN, 1964). Also, the original thickness of shells or carapaces may be

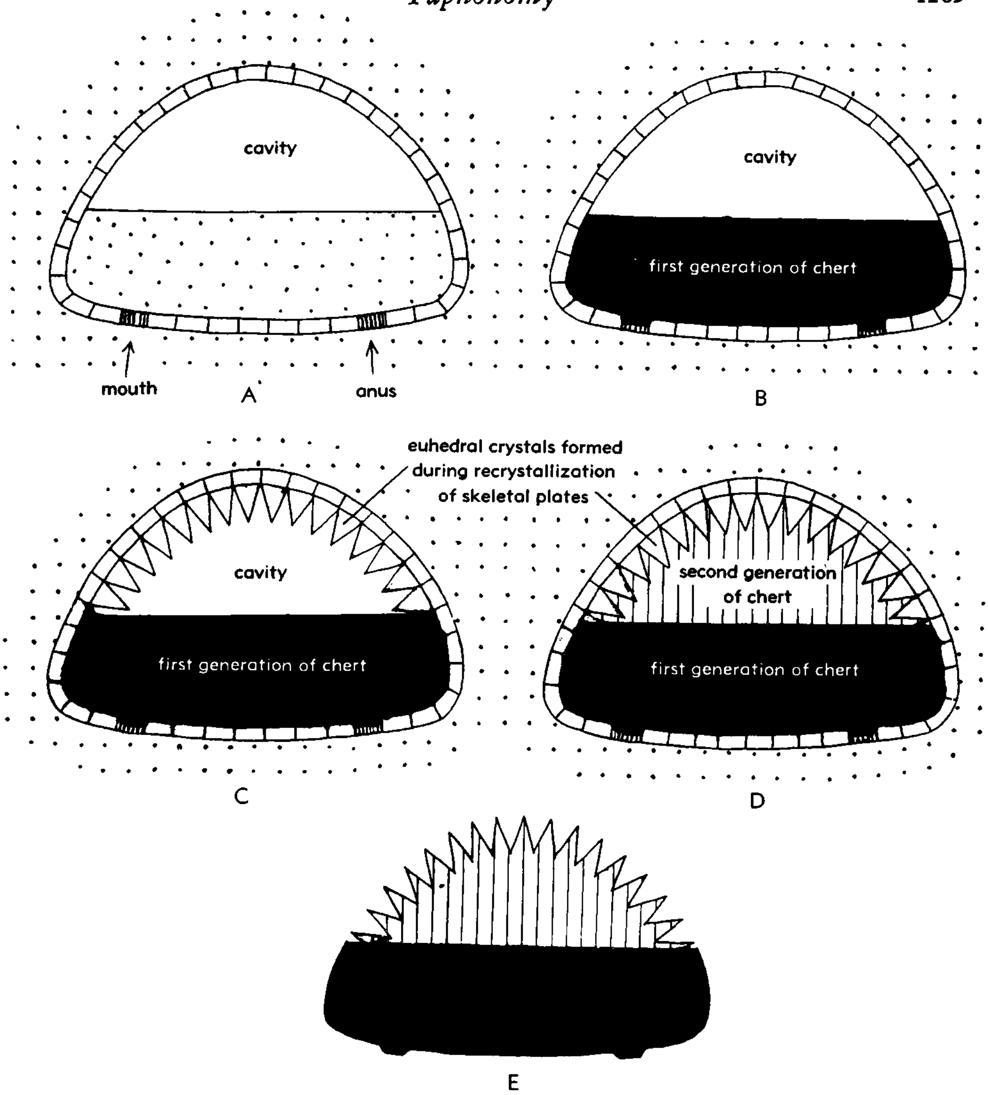


FIG. 51. Schematic diagram demonstrating concretion development *(A-E)* similar to that in Fig. 50 (Müller, n).

altered by recrystallization, and occasionally a considerable increase in thickness can result.

FORMATION OF CONCRETIONS (GEODES) AND THEIR IMPORTANCE IN FOSSILIZATION

Concretions can be divided into three separate groups, according to the time of their formation:

1) *Syngenetic*: formed during sedimentation, frequently characterized by excellent preservation of organic remains within the concretions.

2) *Diagenetic*: formed either shortly after the initial deposition of the sediment or somewhat later.

3) *Epigenetic*: formed after deposition of the surrounding sediment, bedding planes passing from the enclosing rock into the concretion.

Concretions that form around organic remains are of considerable interest to the paleontologist, because they are commonly formed before the initiation of plastic deformation, caused by sediment settling (e.g.,

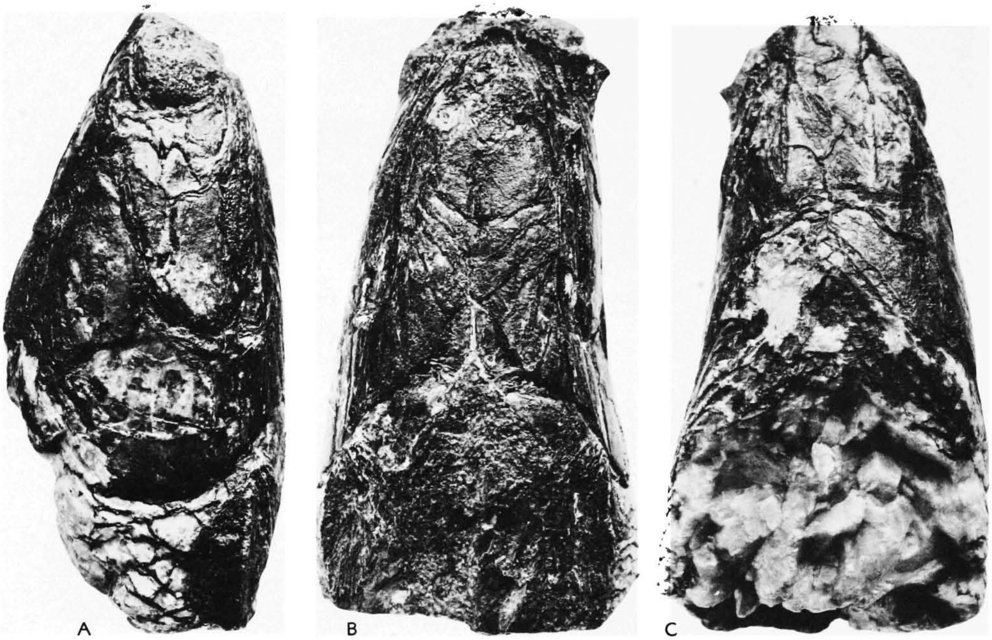


FIG. 52. *Palaeoniscus macropomus* AGASSIZ, with head and anterior part of torso preserved, of early diagenetic, calcareous concretion *("Ilmenauer Schwiele")* (Müller, 1962a).——*A*. Right side.——*B*. Ventral side.——*C*. Dorsal side. Upper Permian (lower Zechstein, Kupferschiefer), Sturmheide b. Ilmenau, Thuringia. Length, 85 mm.

MÜLLER, 1962a; ZANGERL & RICHARDSON, 1963; ZANGERL, 1971). This is also shown by the fact that the interiors of many enclosed fossils contain voids or infillings of unconsolidated sediment. If fossils inside concretions are deformed, it must be concluded that the concretions were formed during or after the settling process.

VOIGT (1968b) described concretions that have grown in several phases conditioned by interruptions in sedimentation or by coalescence of concretions of different ages and called these "hiatus concretions." In some cases, concretions may be exposed and corroded or bored on the seafloor. When sedimentation resumes, growth of the concretions continues (KENNEDY & KLINGER, 1972). This is true for concretions formed syngenetically or by early diagenetic processes in which the organisms around which the concretions grew are well preserved, in many cases with soft parts, or at least their impression.

The material for concretionary growth moves either actively by diffusion or passively with the pore water through the sediment. First of all, the possibility of material migration by diffusion is considered.

Concretions of syngenetic and diagenetic origin are commonly closely connected to the presence of organic remains that form the center of the concretions.

"Thin-walled" concretions tend to outline the enclosed objects. "Thick-walled" concretions tend to be more rounded. Spherical concretions are formed under conditions of hydrostatic pressure. Flattened concretions are commonly formed in connection with inhomogeneities within the sediment, caused by compaction.

It is possible to determine the relative time at which a concretion began to develop by comparing the amount of compaction in the surrounding rock with the degree of deformation of the organism contained within the concretions. Fossils preserved in strongly compacted sediments tend to be completely flattened along bedding planes or when they are attached to the surface of concretions; however, within concretions fossils are usually well preserved, displaying many morphologic details (Fig. 52), because the top of the concretion either protrudes through the sediment surface or merely has less sedimentary load on it because of its geometry. A slow rate of formation of a concretion is indicated, if, for example, the inner volutions of an ammonite shell at its core are better preserved than the outer ones. In this case, the outer whorls were exposed to corrosion by pore water for a longer time than the inner ones.

In some cases, the destruction of fossils by diagenetic processes is obvious. Illies (1949) observed such occurrences in Eocene deposits near Havighorst, Schleswig-Holstein, West Germany, where a bivalve plaster could be traced through several concretions in one bed where the fossils in the surrounding rocks had been completely destroyed. Apparently, these concretions developed before the shells buried in the surrounding sediments were destroyed.

Concretions containing fossils may be split by shrinkage cracks and the fragments displaced vertically or horizontally. Internal shrinkage cracks develop if the concretion consists of a considerable amount of clay or other material of little coherence and high water content. The resulting cracks run either radially or concentrically, and commonly follow the inner and outer boundaries of shells. The subsequent dewatering resulting from irreversible chemical processes leads to formation of shrinkage cracks that are then filled by mineral precipitation (Fig. 53).

The inner whorls of planispiral ammonites may become detached during this process and shrinkage cracks can develop covered by several generations of matlike overgrowths of calcite. Such overgrowths of calcite can make the thickness of the inner whorls appear greater than the outer whorls by more than a millimeter (Hollmann, 1968a). Because it is difficult to distinguish between the steinkern and the calcite filling within these diagenetically produced voids, the impression may be created that the size of the shell is due to anomalous growth (Fig. 54).

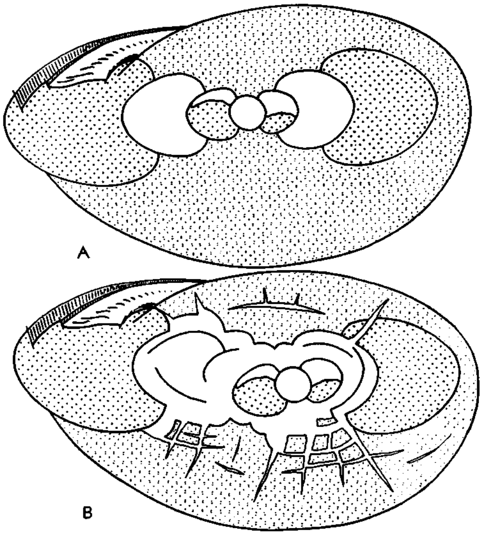


Fig. 53. Cross-sectional, schematic view of septarian concretion with enclosed ammonite (Hollmann, 1968a).——*A.* Prior to the development of shrinkage cracks, camerae serve as "bubble levels."——*B.* Radial and concentric shrinkage cracks have formed from dewatering of the clay minerals which are later filled with mineral precipitates. These cracks commonly conform to inner boundaries of the shell.

TRANSFORMATION OF POLYMORPHOUS SUBSTANCES INTO STABLE MODIFICATIONS

A common process during diagenesis is the transformation of minerals into their more stable polymorphs. Perhaps the most important of these transformations is the inversion of aragonite to calcite. This is important because aragonite occurs in the skeletal material of many organisms, such as corals, scaphopods, gastropods, bivalves, nautiloids, ammonoids, and otoliths (Hall & Kennedy, 1967; Kennedy & Hall, 1967; Kennedy & Taylor, 1968). It has been demonstrated that synthetic aragonite, in water at 40° C, can invert to calcite within a few hours (Wray & Daniels, 1957); however, organically precipitated aragonite can be preserved for long periods of time.

Aragonite is frequently preserved in fossils of Cenozoic age and more rarely in Mesozoic forms. Commonly, such fossils are preserved in muddy or marly sediments. For example, aragonite is preserved in corals of the marly Triassic Zlambach beds and

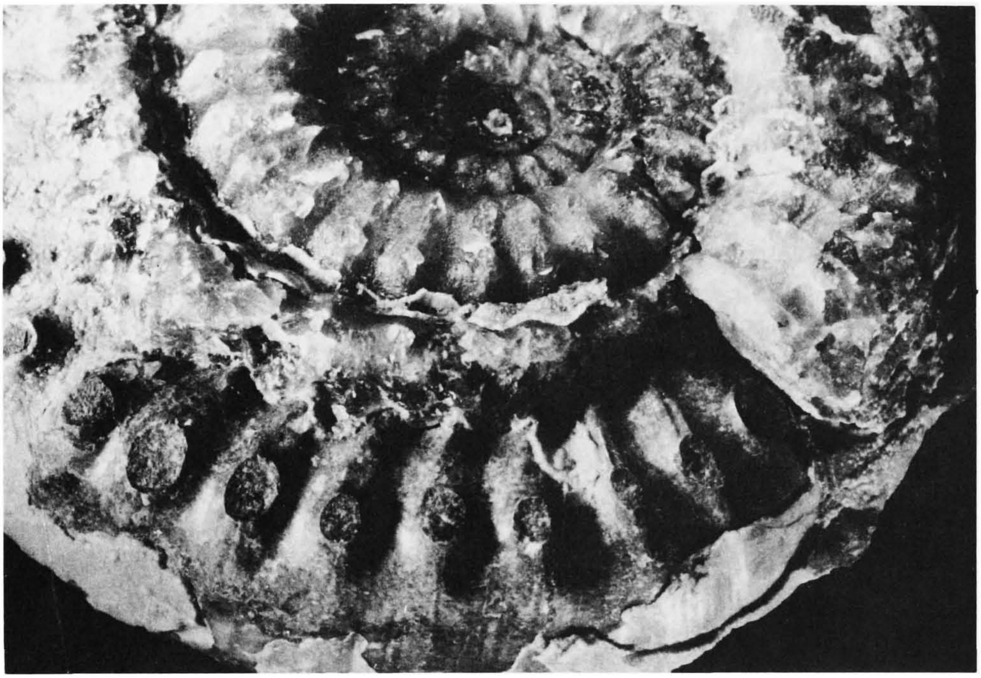


FIG. 54. *Microderoceras birchi* (SOWERBY), a so-called double ammonite; shell of the steinkern is 8 mm thicker than that of the shell, void between the two filled with calcite. Middle Liassic (lower Pliensbachian), Lyme Regis, Dorset, England. Diameter of ammonite approx. 11 cm (Sektion Geowissenschaften, Bergakademie Freiberg, 249/7; Müller, n).

in the hinge of hippuritids of the Cretaceous Gosau beds, both of the eastern Alps (ZAPFE, 1936). There is an apparent correlation between the preservation of aragonitic material and the surrounding sediments. Aragonite is almost totally absent from hard parts in Upper Cretaceous limestone that is poor in organic substance, but is quite common in the organic- and pyrite-rich shales of the Gault.

Aragonite is exceedingly rare in Paleozoic sediments, but is found under special types of preservation. Examples exist in the Kendrick Shale (YOCHELSON *et al.,* 1967), the Buckhorn asphalt in the Pennsylvanian of North America (STEHLI, 1956; LOWENSTAM, 1963; GRÉGOIRE & TEICHERT, 1965), and in the Upper Oil Shale Group (Lower Carboniferous) of Scotland (HALLAM & O'HARA, 1962) in which the clayey matrix contains up to 2.9 percent carbon.

It can be concluded, therefore, that fossil aragonite is best preserved in marly, muddy, and bituminous sediments (HALL & KENNEDY, 1967; KENNEDY & HALL, 1967; KENNEDY & TAYLOR, 1968). Water acts as a catalytic agent in the conversion of aragonite to calcite, and it is the organic material, the conchiolin, which surrounds the individual crystals of the shell, that protects the aragonite. Experiments have shown that dry organic aragonite is stable for an almost infinite period of time, whereas in the presence of water at 10° C., it will invert to calcite in a few million years, and in water at 50° C., in 100,000 years (BROWN *et al.,* 1962). GRÉGOIRE (1959a,b) studied the chemical and structural composition of the organic material of recent mollusks and discovered its composition to be water-insoluble keratine, which completely surrounds the aragonite crystals. This material is rapidly broken down into amino acids that are water-soluble. ABELSON (1957) found that the proteins in the shells of Pleistocene specimens of *Mercenaria mercenaria* had degenerated to peptides and amino acids, and that in Miocene forms only residual amino acids were present.

The stabilizing effect of organic substances is also shown by the occurrence of aragonite in the Wealden beds of the Dalum oil field (northwest Germany), where aragonite is found in the shells of cyrenids and gastropods that apparently had been engulfed by oil or were embedded in clay very early in their diagenetic history (Füchtbauer & Goldschmidt, 1964). The same kinds of shells in clay-free, permeable sediments are completely calcitized. It is probable that very early migration of oil occurred, because the coquinas have high porosity and are underlain by highly bituminous shales that probably represent the source rock.

The conversion of aragonite to calcite leads to the destruction of fine structures within the hard parts of organisms, and all that usually remains are relicts of the original shell structure (Bathurst, 1967; Folk, 1965). During this process, both color and structure of the shell can change. The original aragonitic shells of ammonites turn glossy white and sparry, or they become micro- to cryptocrystalline with a transparent, light-brown color. The original lamellar structure of the shell is preserved only indistinctly.

METASOMATISM OF FOSSILS

Metasomatism can be defined as the gradual replacement of one mineral by another mineral of a different chemical composition (e.g., the replacement of calcite by quartz or vice versa), which occurs frequently during fossilization. If a molecule-for-molecule replacement takes place, the fine structure of the shell is generally completely preserved. If the morphology of the shell is preserved, the process is called pseudomorphism. Commonly metasomatism results in volume changes, accompanied by expansion, folding, compression, cracking, and porosity changes. Occasionally, such changes may be responsible for misidentifications of fossils.

Metasomatism is often a selective process, which may result in the replacement of unstable minerals by more stable ones (Ogose, 1956; Paine, 1937). An example is dolomitization, a process during which aragonitic skeletal parts are affected first, then the rock matrix, and, finally, any parts consisting of original calcite; however, this process is usually accompanied by loss of fine shell structures (for exceptions see Papp, 1939).

Frequently, calcium carbonate is replaced by pyrite or marcasite (Gripp & Tufar, 1965). This process always begins on the surface of the fossils and takes place if acid solutions containing iron ions and hydrogen sulfides react with the carbonate and become neutralized. An example of pseudomorphism of cassiterite (SnO_2) after calcite are crinoid stems in the Permian limestone in the Emmaville district, New South Wales, Australia. The metasomatism was caused by the migration of elements from the Upper Permian granite body, which impregnated the surrounding rocks with cassiterite-containing quartz (Lawrence, 1953).

PRESERVATION OF STRUCTURAL SOFT PARTS

Although paleozoology has historically been concerned with the investigation of perservable hard parts or organisms, the preservation of soft parts with fine organic structures is by no means unusual. The following examples are well known: 1) preservation of delicate soft parts and appendages in the Middle Cambrian Burgess Shale, British Columbia (see Whittington, 1971, for earlier literature); 2) preservation of appendages and soft parts of Cambrian and Ordovician trilobites (Raymond, 1920); 3) preservation in limonite-goethite of soft-bodied worms in the Devonian of New York (Cameron, 1967); 4) preservation in pyrite of soft parts of Devonian cephalopods (Stürmer, 1969, 1973; Rietschel, 1968; Zeiss, 1969); 5) preservation of various soft parts of Mesozoic ammonoids, e.g., egg cases (?) (Lehmann, 1966; Müller, 1969b), ink sacs (Lehmann, 1967b), crop and gills (Lehmann & Weitschat, 1973); 6) remains of soft parts in the Solnhofen Limestone of Bavaria (Reis, 1893); 7) phosphatized ostracodes from Lower Cretaceous (Aptian, Albian) freshwater beds of Brazil with completely preserved musculature and male sexual organs preserved in the erectile position (Bate, 1971); 8) soft parts and

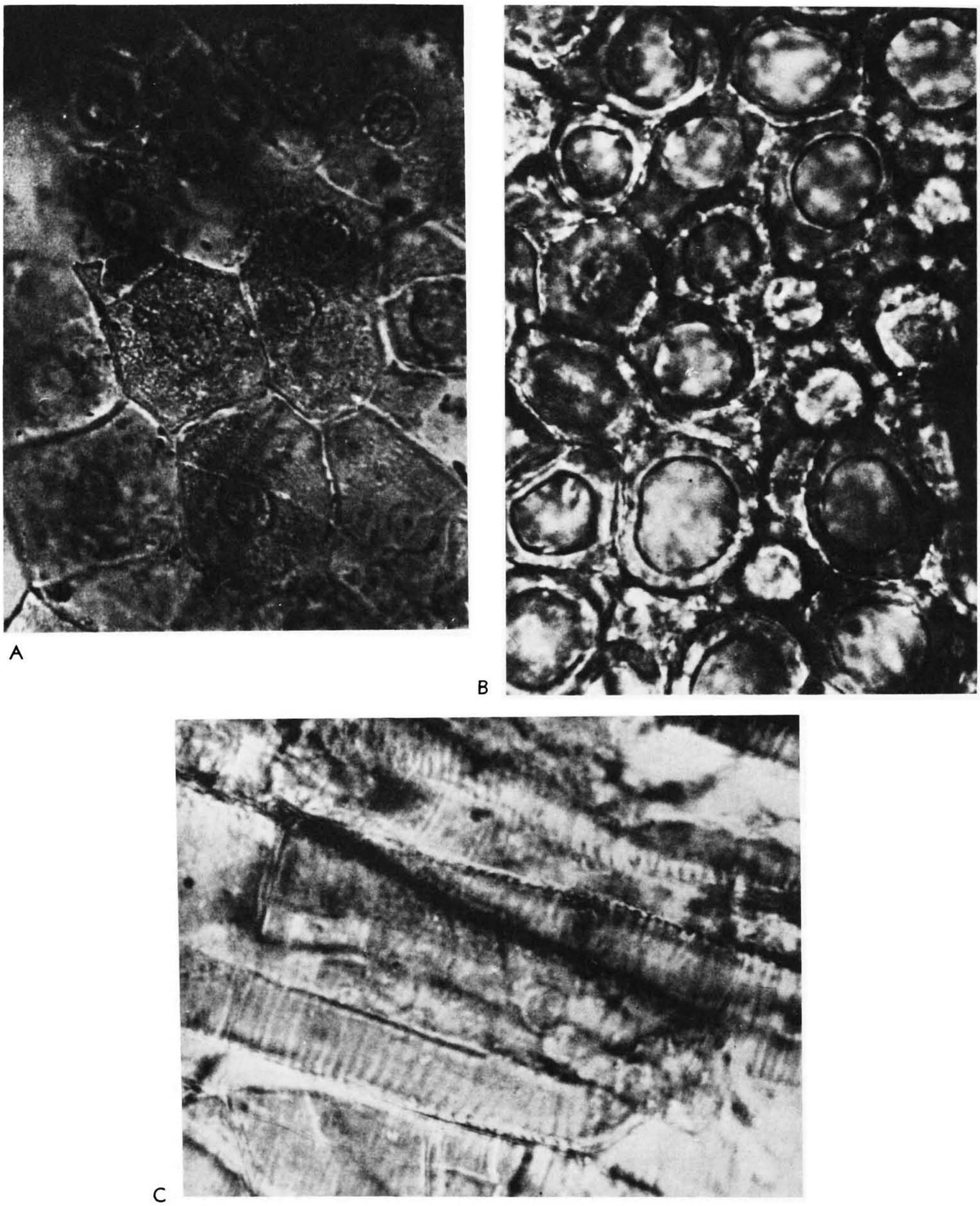


FIG. 55. Preserved soft parts of organisms from Middle Eocene Brown Coal, Geisel Valley near Halle/Saale.——*A.* Large, plate-like epithelial cells, with nuclei, from a frog epidermis, ×747 (Voigt, 1935).——*B. Cecilionycteris prisca* Heller, connective tissue in the ear, ×900 (Voigt, 1936).——*C.* Parallel trachea of *Eopyrophoras* sp., ×900 (Voigt, 1938b).

fine organic structure from the chalk of Europe (W. Wetzel, 1913, 1937); 9) soft parts from the Eocene brown coal of the Geisel Valley near Halle (Voigt, 1935; 1936; 1938a,b; 1950; 1956; 1957; H. Brenner, 1939); 10) soft parts preserved in amber (Voigt, 1937, 1938c) and similar fossil and subfossil remains (Bachofen-Echt in Abel, 1935; p. 601-619; Lazell, 1965; Schlee, 1973); 11) mummified ostracodes in the Pleistocene of Alaska (Schmidt & Sellmann, 1966).

PRESERVATION OF SOFT PARTS IN EOCENE COAL

Specimens preserved in the Eocene brown coal of the Geisel Valley near Halle have been extensively investigated by VOIGT (1936; 1938a,b; 1950; 1957) (Fig. 55,*A-C*). With the exception of mumified remains known from Pleistocene and younger deposits, this material shows better preservation than that from any other locality. The Eocene fossils were preserved in bogs, and it is believed that the soft parts were preserved by acidic waters in the absence of bacteria and oxygen. The bones were preserved because of the neutralizing effect of calcium carbonate solutions. In some, soft parts such as muscles and corium, secondary silicification has been observed. As a rule, the tissues of smaller animals were best preserved, because solutions with dissolved minerals were able to penetrate them more rapidly than those of larger organisms. An example is the preservation of the delicate skin of frogs, whereas physically more durable structures, such as hooves, beaks, and horns were not preserved. The following soft parts have been found and studied microscopically: fat cells of reptiles and mammals; epidermis of frogs, bats, and artiodactyles; different types of mammal hair; the connective tissue of the corium of fish, frogs, reptiles, and mammals (Fig. 55,*B*); epithelial cells with nuclei of frogs (Fig. 55,*A*); melanophores of frogs and fish; blood vessels with erythrozytes of lizards; hyaline cartilage with cartilage cells of hyracotheriids; musculature of roaches and crabs, fat cells of roaches and larvae of Diptera.

Such observations are especially valuable if they yield diagnostic features that cannot be seen in hard parts alone. One of the few fossil representatives of the Nematophora, *Gordius tenuifibrosus* VOIGT, was accidentally discovered on the basis of the structure of a single, 15 mm-long fragment of subcuticular tissue (VOIGT, 1938a).

PHOSPHATIZATION OF SOFT PARTS

The phosphatization of soft parts is rather sporadic in occurrence, and found in sedimentary deposits since the Early Carboniferous. Typically, fish are preserved in this way, especially the musculature, stomach and intestinal contents, cutis, testicles, and spinal cord.

REIS (1893) studied in great detail the phosphatized musculature of worms (annelids), coleoid cephalopods, insects, fish, and reptiles from the Solnhofen Limestone.

REIS described the fossilization of organic material by phosphate which he called *Myo-* and *Zoophosphorit.* The composition of the material was about 70 percent $Ca_3P_2O_8$ and 6 to 6.5 percent CaF_2.

Specimens in the Solnhofen Limestone, on the other hand, are composed of 97 to 98 percent $Ca(MgK_2Na_2)CO_3$, small amounts of SiO_2,Al_2O_3, and so on, traces of P_2O_5 and no fluorite. It is quite obvious that the limestone itself does not contain sufficient $Ca_3P_2O_8$ and CaF_2 for phosphorization of fossils and, therefore, these minerals must have been concentrated by diagenetic processes. These have been found together with the abdomens of embedded cadavers of flesh- and bone-eating animals such as sharks, bony fish, and dibranchiate cephalopods. In these, the phosphorization of muscle tissue is most common; however, the carnivores of the genus *Lepidotus* and the pycnodontids are very seldom phosphorized. Phosphorization has never been observed in cephalopods with external shells.

Pyritized soft parts of ectocochleate cephalopods (orthocerids, bactritids, goniatites) have been discovered by X-radiography in Middle Devonian Wissenbach Shale of Germany, especially the intestines, funnel, and arms (STÜRMER, 1967, 1968a, 1968b; ZEISS, 1969). The intestines, especially the terminal part, are longer than those of living cephalopods, though generally similar in morphology. The arms of coiled forms are more strongly differentiated than those of orthoconic forms possessing an umbrella-like sail of which the arms are extensions. In one case more than 10 arms have been observed, supporting the conclusion that, judging from the number of their arms, the ammonoids, bactritids, and probably also the orthocerids have to be included in the dibranchiate coleoids. This conclusion is supported by finds of heterodont radulae in Paleozoic and Mesozoic ammonoids (CLOSS, 1967; LEHMANN, 1967a) as well as by arguments presented by TEICHERT *et al.* (1964).

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