N.]	Jb. Geol. Paläont. Abh.	152	3	307356	Stuttgart, November 1976
------	-------------------------	-----	---	--------	--------------------------

Fossildiagenese Nr. 20*

Preservational history of compressed Jurassic ammonites from Southern Germany

By

A. Seilacher, F. Andalib, G. Dietl and H. Gocht

With 20 figures in the text

SEILACHER, A., ANDALIB, F., DIETL, G. & GOCHT, H.: Preservational history of compressed Jurassic ammonites from Southern Germany. — N. Jb. Geol. Paläont. Abh., 152, 307—356, Stuttgart 1976.

Abstract: Preservational features express the varying time relationships between shell solution, compaction and cementation processes during early diagenesis. In many cases they correlate better with the depositional environments than with the present lithologies of the enclosing rocks.

Key words: Ammonitida, fossilization, diagenesis, deformation, Jurassic; SW-German mesozoic hills.

Zusammenfassung: Erhaltungszustände definierter Gehäusetypen spiegeln das zeitliche Verhältnis von Schalenlösung, Kompaktion und Zementation während der Frühdiagenese. Da sie eher vom Ablagerungsmilieu als vom Stoffbestand des fertigen Gesteins abhängen, können sie als Fazies-Indikatoren eingesetzt werden.

The beauty of fossils is one of the main attractions in paleontology; but at the same time it tends to distract from the wealth of geologic information that is encoded in the "poor" specimens. The present study tries to tap this reservoir by using ammonites so poorly preserved that they would have been rejected by most collectors.

This project forms part of the program "Fossil-Diagenese" in the Sonderforschungsbereich "Palökologie", Tübingen. Support by the Deutsche Forschungsgemein-

^{*} Nr. 19: J. NEUGEBAUER: Preservation of ammonites. — In: J. WIEDMANN & J. NEUGEBAUER, Lower Cretaceous Ammonites from the South Atlantic Leg 40 (DSDP), their stratigraphic value and sedimentologic properties, Initial Reports Deep Sea Drilling Project, 40, im Druck.

schaft is gratefully acknowledged. Thanks are also due to the participants of our Tübingen "Rundgespräch" on the diagenesis of fossils, Febr. 19./20. 1972, who by their discussion contributed to the clarification of the problems. Some of the data presented have already been included into a more general contribution (SEILACHER, in press).

The subject has also gained from discussions following lectures of the senior author in Braunschweig, Erlangen, Glasgow, Buenos Aires, Mexico City, Miami, Stanford and Cairo.

We are indebted to Prof. G. EINSELE (Tübingen) for critical remarks about the deformational behavior of soft sediments and to Prof. H. PUCHELT (now Karlsruhe) for geochemical analyses through a Holzmaden dome ammonite. Dr. F. VIOHL allowed us to make use of the collections in the Eichstätt theological seminar and J. FI-SCHER (Holzmaden) genereously provided interesting specimens from his shale quarry.

Unless stated otherwise, specimens are deposited in the collections of the Department of Geology and Paleontology, University of Tübingen, catalogue numbers GPIT 1489/1-61.

I. Introduction

Due to their morphological complexity and to their occurrence in a variety of lithofacies, ammonite shells have for more than a century played a prominent role in phylogeny, biostratigraphy and paleogeography. By the same virtues they can be used as sensitive test bodies for the sedimentational and diagenetic processes to which they were exposed after the death of the ammonite animal.

Previous studies on ceratite preservation in the Muschelpalk (SEILACHER, 1971) have revealed a large variety of case histories reflecting the interplay of buoyancy, internal sedimentation, burial, prefossilization and reworking prior to the final emplacement of the shells in the sediment. In contrast to the s e d i m e n t a t i o n a l (i. e. biostratinomic) history, however, the diagenetic aspect of ceratite preservation is rather monotonous: In the Muschelkalk muds, the periostracum as well as the aragonitic shell layers were dissolved very early in diagenesis. Only those shells survived in the record whose sedimentary filling had still earlier become cemented by concretionary processes (see p. 344). Other preservational expressions, such as flattened specimens, shell sherds, and even growth lines, are virtually unknown in Muschelkalk ceratites.

Ammonite preservation in red nodular limestones from the geosynclinal realm (NEUMANN & SCHUMANN, 1974) illustrates an interesting modification of the ceratite model: Again, early concretionary cementation of the fill sediment, followed by complete shell solution and eventual pressure solution, is the dominant diagenetic process. In this case, observed deviations from the ceratite model can be referred to differences in the sedimentological and the diagenetic regime (SEILACHER, in press, Fig. 19): a) Lower turbulence and survival of the phosphatic siphuncle (ANDALIB, 1971) reduced draught filling, so that the phragmocones remained largely empty except in damaged shells.

b) The slow rate of sedimentation has allowed the body chamber fill to reflect changes in deposition, and the whole shell to reenter sedimentation in a pre-fossilized state without displacement. If the exhumed specimens had already lost the shell walls, secondary internal sedimentation could now fill open spaces that had not been previously accessible. The steep diagenetic gradient also allowed compressional deformation of the steinkerns over underlying nodules that had already been hardened.

c) The shell geometry of bullate forms allowed the deep upper umbilicus to act as a trap for bioclastic particles which became prefossilized along with the material trapped in the body chamber. Bullate geometry also explains why the body chamber steinkerns got often deformed, by breakage and internal pressure solution, during later stages of compaction.

Though being more complicated, the preservational record of the nodular limestones is still incomplete, since it largely excludes shell sherds and shells that had became crushed previous to the concretionary steinkern formation.

The diagenetic history, with which we are here concerned, is more fully decipherable in sediments in which the shell wall itself, or at least its periostracal coating, has survived long enough to leave a lasting imprint in the rock. This is the case not only in coarse sediments that were already lithified before compaction could become effective, but also in pelitic sediments with a high sealing effect. Sedimentologically, the pelitic facies usually corresponds to lower energy environments. Therefore, in comparison to the Muschelkalk example, the shells have rather monotonous sedimentational histories: They have rarely become buried in upright landing positions, or sediment filled. With few exceptions, the shells entered diagenesis without previous reworking, with empty phragmocones, and in horizontal positions. But their biostratinomic monotony also facilitates the reconstruction of subsequent diagenetic events, which affected the shell mainly through the following processes:

a) microbiological degradation of organic shell substances.

b) mechanical deformation which, depending on the state of shell solution, may or may not be connected with fracturing.

c) chemical processes causing:

- 1. Shell solution by pore fluids.
- 2. Shell support by cementation of the whole sediment or of localized concretions.
- 3. Filling of internal cavities with pyrite and/or drusy calcite.
- 4. Recrystallisation of the shell.

To some degree the chronological sequence and interrelationship of these processes can be reconstructed from preservational features. The cases presented in this paper reflect mainly the varying interplay of shell destruction by solution, shell deformation by compaction, and shell conservation by cementational processes.

For a comparative study of ammonite preservation, the classical Jurassic sequence of southern Germany with its great environmental and lithologic diversity is particularly suited. It allows to test the correlation of the preservational types not only with the present lithology, but also with the environmental character of the enclosing rock. The preservational features may also reveal details of the early diagenetic history of a particular sediment, including porosity and permeability. This paper concentrates on compressed ammonites, which have been largely neglected by paleontologists because they are little "attractive" and fail to show taxonomically important details such as suture lines, original shell geometry and early ontogenetic stages. Although our material comes from only a few lithotopes (black clays, bituminous shales, lithographic limestones), a surprising variety of preservations has been found. Our data can probably be duplicated and elaborated in other sedimentary series. We also hope that our predominantly morphological studies may stimulate and direct supplementary geochemical surveys that are needed for a more complete understanding of diagenesis.

Since our study includes the Posidonia Shales and the Solnhofen Limestones, it also contributes to the theme "Fossil-Lagerstätten". In this respect, the accumulation of new data, however contradictory, seems to us more promising than the fight over established environmental models, none of which fits these data completely. Only from the synthesis of stratigraphic (Oil Shale Group, Tübingen), sedimentological (HEMLEBEN, in preparation), taxonomic (GRÜN, 1975; GROISS, 1967), synecological (KAUFFMAN, in preparation), biostratinomic (BRENNER, 1976) and geochemical details (VEIZER, in press) can we hope for a conceptual break-through.

II. Normal compressional sequence

Chemical solution and compactional deformation of the aragonitic shell are the two main processes, whose interplay determines ammonite preservation in pelitic sediments. They are counteracted by the mechanical strength of the shell, which is in part defined by the shell geometry. Therefore we shall discuss the preservational phenomena separately for the main shell types represented.

A. Harpoceras type

Oxycone shells have evolved independently in many groups of the ammonites, because they optimise lateral butressing of the phragmocone wall by fluted septa against water pressure (SEILACHER, 1975). Since dead

Preservational history of compressed Jurassic ammonites

shells of this type are almost invariably buried in horizontal position, it so happens that the phragmocones are also very strong against the compactional stress. The body chamber, in contrast, was not designed as a pressure vessel and was ill-suited to resist the lateral stress in a compacting sediment. Therefore we may expect that the preservational difference between the two shell sections is larger in this than in other geometric types.

1. Compression in Amaltheus

The Amaltheus Shales represent the "ordinary" type of Jurassic dark shales. Their fauna is largely benthic with *Chondrites* and other burrows, serpulids, gastropods, pelecypods, brachiopods and echinoderms, all of comparatively small size. Nectonic cephalopods (ammonites, belemnites) are also common. Since turbulence was relatively low in this environment, only the ammonites' body chambers became sediment-filled, while most of the phragmocones remained empty. Nevertheless, even the discoid *Amaltheus* shells were usually spared from compactional deformation because their open phragmocone chambers had become reinforced by pyrite linings and drusy calcite at an early stage of diagenesis. Also, the shell aragonite did not become dissolved, but transformed into calcite at a later stage.

a) Pyrite linings:

Framboid pyrite linings are probably the result of bacterial sulfate reduction (HUDSON & PALFRAMAN, 1969). As such, they may reflect living conditions immediately below the sediment/water interface.

In addition, they can be used as geopetal structures: In vertical sections (Fig. 1), the pyrite linings show minute projections on one side of the cavities but not, or much less pronounced, on the other. A check against incomplete fillings shows that their similarity with icicles or stalactites refers also to their orientation.

Leaving aside the genetic problems, the geopetal labelling by "stalactitic pyrite" can be used not only to determine the original position (top and bottom; oblique; vertical) of loose shells more commonly and more exactly than with incomplete fillings. They may also help to recognize paleoslopes or secondary changes in orientation by tectonics, differential compaction, slumping, or reworking, if the position of the fossils has been measured in the field.

In the present study, we have used the stalactitic pyrite only for flat lying *Amaltheus* shells that did become compressed in spite of their pyritic reinforcement (Fig. 1). In such specimens it becomes clear that the collapse happened after the pyrite, and before the drusy calcite, formation, because in the shell fragments tilted during the collapse, the



Fig. 1. Parallel sections through pyritized *Amaltheus*. Neither the collapse (A; arrows) nor the umbilical phosphate concretions (P) are geopetal; but the close-up (B) reveals truely geopetal structures (pyritized partial fill, F; stalactitic pyrite linings) and the following time sequence:

- phosphatic concretions (holding burrows open).
- pyritisation in open spaces (burrows in concretion; septarian cracks at concretion/shell contact; pores in spiral layer; pore spaces in coarse fill sediment; walls of empty chambers).
- compactional collapse (fragments with stalactites tilted; fracture surfaces free from pyrite).
- drusy calcite fills remaining cavities.

Lias delta (Domerian); Holzheim; GPIT 1489/1.

All scales are 1 cm, unless stated otherwise.

pyrite does not heal the fracture surfaces and the stalactites are tilted accordingly. Also, the collapse was not geopetal since either the upper or the lower side may be broken-in.

b. Phosphatic concretions:

In many specimens the body chambers have remained uncollapsed due to the concretionary hardening of their fill sediment. The brownish colour and analysis indicate that these concretions were largely phosphatic. Often sediment has also entered — probably through leaks — into the innermost whorls of the phragmocone. In this place, however, the concretionary cementation tends to protrude outside the shell. In this way we explain the umbilical cushions, which may be on the lower or the upper, or on both, sides of the shell (orientation by stalactites). In other areas (Schnaittach, Franconia; specimens from Prof. ZEISS, Erlangen GPIT 1489/55) these cushions have grown into concretions larger than the shells. Their lopsidedness away from the body chamber probably results from an originally oblique position of the shell, with the body chamber at the bottom.

It is of particular interest that pyrite-lined burrows are found within, but not outside, the concretions. Also, a thin pyritic lining on the outer surface of the shell is restricted to the central part of the umbilical concretion (Fig. 1, B). Hence we conclude that the concretionary cementation started before the pyrite formation, providing uncollapsed burrows and septarian cracks for the bacterial activity.

Results:

- 1. In the Amaltheus Shales internal sedimentation was usually restricted to the body chamber and leaking parts of the inner whorls.
- 2. The shell aragonite did not dissolve but later transformed into calcite.
- 3. Phosphatic concretions were formed in the body chamber, in the sediment-filled innermost whorls and in the umbilical depression, but without consistent geopetal orientation.
- 4. After the concretionary cementation, but still very early in diagenesis, bacterial activity produced framboid pyrite linings in the empty phragmocone chambers and in the cavities held open by the concretion. These linings are geopetal, forming vertical microstalactites in the roofs of the cavities.
- 5. These processes occurred close to the sediment surface, providing resistant ammonite fossils that could survive subsequent reworking and compaction without deformation.
- 6. The exceptional collapse of hollow phragmocones occurred after pyrite, but before drusy calcite, formation and was not geopetal.

2. Two-phase collapse in Leioceras opalinum

In the dark clays of the Lower Dogger in Southern Germany, Leioceras opalinum has often preserved the original aragonite shell and even the nacreous lustre, to which the species name refers. Secondary shell calcitisation is usually restricted to the top parts of the sequence (ANDA-I.IB 1970, 1973), but may locally reach down to the *torulosus*-zone. In such places we find what is here called "beer mat" preservation. It is not directly related to the calcitisation and is probably just as common where the shells are still aragonitic. But only where later recrystallisation has reinforced and welded the broken parts together, can entire "beer mats" be picked out of the rather soft clay.

The following observations are based on hundreds of loose specimens in the Tübingen museum. They were collected in the last century, and in excavations made after the locality in the Steinlach stream bed near Mössingen had been re-discovered by the joint efforts of F. LÖRCHER (Dotternhausen) and TH. KELLER (Frankfurt).

a) Longitudinal fractures:

The fracture lines in a collapsing ammonite are to some extent determined by the shell geometry. Minor fractures that more or less follow the ammonite spiral tend to form in the middle of the whorl flanks. More prominent "keel fractures" (Fig. 2, B) are commonly found right



Fig. 2. In discoid shells, the body chamber collapse produced angular sherds-that pierced laterally under more resistant structures (umbilical shoulder; keel ring; phragmocone). The phragmocone collapse occured at a later stage. In contrast to the phosphatic concretion in Fig. 1, the pad of cone-in-cone calcite (hatched; non-geopetal) has formed after the phragmocone collapse.

A. Posidonia Shales (Toarcian); Holzmaden; GPIT 1489/2.

B. Opalinus Clay (Aalenian); Mössingen; GPIT 1489/3.

beside the keel which forms a reinforced structure throughout the shell. Therefore another fracture zone has often formed where the rigid keel from the next inner whorl presses against the collapsing outer whorl ("superimposed keel fracture"). In many cases the steep umbilical shoulder has acted as another rigid structure ("umbilical fracture").

Since fractures are often asymetrically developed on the two flanks, we first suspected them to be geopetal. But field observations have shown that this is not the case. This strongly indicates that the shells collapsed under equal pressure from both sides, i. e. under a considerable sediment cover.

b) Telescope fracture:

Although beer-mat shells show the same type of deformation in the body chamber and in the phragmocone, the boundary between the two



Fig. 3. "Beer mat" preservation (see Fig. 2, B). While fracture patterns are similar throughout the shell, the telescope fractures (arrows) on both flanks (optically inverted) indicate a two-phase collapse.

Lower Opalinus Clay; Mössingen. A, B: Leioceras opalinum; C: Lytoceras torulosum; GPIT 1489/4-6. sections is in most specimens marked by a prominent radial fracture passing into the umbilical fracture of the body chamber (Fig. 3). Like the longitudinal fractures, it is developed on the upper as well as on the lower side; but unlike other radial fractures, it is asymmetrical in that it always forms a marked cuesta towards the body chamber.

Cross sections reveal that this cuesta is caused by minor but regular telescoping of the body chamber into the phragmocone (Fig. 2, B). This goes along with the assumption that the body chamber, lacking septal support, should collapse first, and that the flattening be compensated by lateral extension of the sherds.

c) Lobe fractures:

Surprising is not the fact that the phragmocone resisted the compaction pressure longer than the body chamber, but that it eventually broke with similar fracture patterns in spite of its septal supports.

Only in a few exceptional specimens did the septa influence the fracturing, though in an unexpected form (Fig. 4). In analogy to the telescope fracture over the last septum we would expect radial, but otherwise rather irregular fractures to form over the previous septa. Instead, the fracture



Fig. 4. Lobe fractures in beer mat specimens of Leioceras suggest later modelling of the softening shell wall against mineralized septal margins underneath (geopetal?). L. Opalinus Clay; Mossingen; GPIT 1489/7-9.

lines follow the individual septal lobes in considerable detail, indicating that the shell wall did no more react as a rigid structure but rather like a mosaik of minute elements. Therefore we conclude that these "lobe fractures" did not form during the original diagenetic implosion of the phragmocone, but represent subsequent modelling of the collapsed shell wall over the pyritized margins of underlying suture lines by a time, when the organic sheaths in the shell structure had disintegrated enough to allow individual displacement of the aragonite crystallites.

Results:

- 1. Leioceras shells in beer mat preservation have suffered complete flattening, because their empty phragmocones did not become supported by concretion, drusy calcite or pyrite; the collapse has happened under considerable sediment cover.
- 2. A two-stage collapse is indicated by the regular telescoping of the body chamber into the phragmocone.
- 3. Fracture patterns in these two parts do not consistently differ in spite of the differences in collapse timing and septal support.
- 4. Recrystallisation of the shell aragonite into calcite and the formation of conein-cone pads (Fig. 2, B) were later processes that did not influence the shell deformation.

3. Harpoceras in the bituminous Posidonia Shales

In the Posidonia Shales (Upper Lias) Holzmaden and other localities, famcus for the perfect preservation of their vertebrate fossils, ammonite preservation is notoriously poor. Not only are all shale ammonite flattened, but the shells have also been completely dissolved withcut replacement, leaving only a brownish periostracal film.

Also spared from this solution where other non-aragonitic parts of the shell, such as aptychi and the calcitic conellae (HÖLDER & MOSEBACH, 1950) that are occasionally found on the deformed floor of the hollow keel in Holzmaden *Harpoceras*, or at the connecting tubes of the siphuncles. The latter seem to have been highly phosphatic and often appear disarticulated due to the solution of the aragonitic linkages (ANDALIB, 1971).

a) Compactional sequence:

Under these conditions it is not easy to detect the cuesta of the telescope fracture; but the two stage collapse is adequately documented by the fracture style:

In *Harpoceras*, which resembles *Leioceras* in geometry, the body chamber also shows similar fracture patterns (Fig. 2, A and 5, A) with sherds presenting a smooth and shiny surface. The collapsed phragmocone, in contrast, has no fractures; at the same time it appears dull from minute wrinkles and irregularities.



Fig. 5. Preservation in Posidonia Shales of Holzmaden.

- A. *Harpoceras:* Even though the telescope fracture is masked by shell solution and compression, the contact between fractured body chamber (well preserved sculpture) and soft-deformed phragmocone (poor sculpture!) indicates a two-phase collapse.
- B. Lytoceras: same contrast, emphasized by body chamber fragments piercing beyond the spiral outline (see Fig. 6).
- C. Dactylioceras: Uniform fracture pattern throughout the shell suggests one-phase collapse in accordance with more stable shell geometry.
- D. Nautilus: Resting on a broad venter, the shell maintained its vertical landing position and became almost unrecognizeable in the compressed state. Fracture patterns of the body chamber indicate a two-phase collapse. GPIT 1489/10-13.

Preservational history of compressed Jurassic ammonites

Suture lines are usually lost in Posidonia Shale ammonites. Only a few Harpoceras specimens (HENGSBACH, 1974) make an exception to this rule, but in a way consistent with our preservational model. In contrast to the lobe fractures of Leioceras (Fig. 4), the sutures appear as soft grooves on the periostracal impression, and only on the lower side of the very last phragmocone chambers. Obviously they had been cast by a thin layer of fill sediment, which by the time of shell solution was hardened enough by pressure shadow cementation (p. 343) to act as a stencil against the soft periostracum.

HOLZMADEN SHALE AMMONITES



Fig. 6. While a two-phase collapse occured in all three genera, only *Harpoceras* preserves the smooth spiral outline of the body chamber, because the resistant keel has caught the spreading shell fragments. Posidonia Shales; Holzmaden; GPIT 1489/14-22.

319

b) How deep in the sediment did the shells dissolve?

In the present Baltic sea, mollusc shells suffer aragonite dissolution at the sediment/water interface. Burial stops carbonate solution, but favors the microbiological disintegration of the organic material (LEWY 1975). In contrast to this model, Posidonia Shale and Solnhofen ammonites indicate that the shell carbonate was dissolved after burial while the organic periostracum remained unaffected.

In the Posidonia Shales, we have only one possible indication for the depth of shell solution: A large surface of the "Seegras-Schiefer", on exhibit in the Tübingen Museum, contains a single flattened *Harpoceras* shell. This shell seems to be perforated by the *Chondrites* burrows. Since *Chondrites* is the work of a soft-sediment feeder that did not burrow deeper than about 20 cm below the sediment surface, this observation would suggest that the shell was already dissolved at this depth.

There are, however, a few reservations to be made. The Seegras-Schiefer marks the transition between an early phase of oil shale sedimentation to a marl with abundant benthic fauna (Aschgraue Mergel). Thus it is possible that a layer of less compacted oil shale was eroded before the bioturbation has started. In this case, the solution level could have been dceper in the sediment. We should also note that more specimens with their counter-impressions would be needed to corroborate this observation. It is in the hope of such future evidence that we mention this potential clue.

Results:

- 1. In the Posidonia Shales, all ammonite shells have become dissolved during early diagenesis in spite of the fact that the rocks are more bituminous and more calcareous than the Opalinus Clay.
- 2. By the time of the body chamber collapse, the outer shell was still a rigid structure that reacted by fracturing; but it became reduced to a flexible foil before the phragmocone did also collapse ("partial leaf preservation", Fig. 5A).

4. Oppelia in the Solnhofen lithographic limestones

In the Upper Jurassic Solnhofen limestones, like in the Holzmaden Shales, the famed perfect preservation does not apply to the ammonites, which occur as flat periostracal impressions on the bedding planes. The periostracal film that has originally protected these impressions, was usually lost some time after rock cementation, allowing the shell surface to become obscured by microscopic stylolitisation. Therefore, details of ornamentation and fragmentation can rarely be seen as clearly as in Holzmaden. In a few Oppelia specimens, the phragmocone parts nevertheless preserve a very thin phosphatic lining, which has also been found in other ammonites (BAYER, 1974; ANDALIB, 1971).

On the other hand, the calcareous sediment has preserved alternative features by which the picture, which we have so far gained of the deformational processes, may be confirmed and elaborated:

a) Apertural plug:

While the phragmocone and the larger part of the body chamber are flattened to partial leaf preservation, the aperture is usually bent up in a peculiar way (Fig. 7). Cross sections show that we deal with a three-



Fig. 7. Oppelia from Lithographic Limestones. As a rule, the shell is exposed on the sole face and flattened, except for a calcite patch behind the telescope fracture and a wedge-shaped apertural plug preserving sculptural details (top pictures).

The corresponding caldera on higher bedding planes (bottom pictures) contours shell and apertural plug, while the two collapse phases are expressed by soft deformation in the body chamber, and microfaulting in the phragmocone, section. Note also the pedestal around the shell and the corresponding marginal sulcus with apertural depression. These features are not found in the Nusplingen facies. GPIT 1489/ 23-25.



Fig. 8 (Legend see p. 323)

dimensional, trumpet-like flaring produced by a sediment plug in the apertural opening (Fig. 8).

In our interpretation the body chamber did not become sedimentfilled originally, possibly because it was still occupied by soft parts. This is particularly plausible for shells in which the aptychi are still preserved; but their plug has the same shape as in shells without aptychi. In any case, the sediment did intrude only after burial, forming a plug with offset layers near the aperture (Fig. 8, C-D) and pushing the aptychi into the secondary position described by SCHINDEWOLF (1958). Much harder to explain is the regular shape of the fossilised plug. In most cases it forms a wedge whose inner edge runs from the ventral corner of the aperture tangentially towards the inner whorl. This line, often accentuated by oblique fractures (Fig. 9), is probably determined not by retracted soft parts, but by the statics of a shell in which only the aperture was supported by sediment. Upon collapse, the plug was still soft and therefore became deformed into a wedge. It also had the effect of sealing the wedge fragments and thereby preserving the ornamentation better than in the rest of the shell (Fig. 7, B).

One may also wonder why only the lower, and never the upper, half of the apertural trumpet is exposed on the bedding plane. But this agrees with the general rule that Solnhofen fossils occur at the bottoms of the turbidite-like calcareous layers and stick to the upper, rather than to the lower, slab if a bedding plane is split open.

b) Calcite puddle:

In addition to the telescope fracture and to the different style of deformation in body chamber and phragmocone (both features are often obscured by stylolitisation), Solnhofen Oppelia shells present two more

Fig. 8. Vertical sections reveal the spacial relationship between different bedding plane features (shaded layers do not differ in sediment character).

A. Concretionary bed, thickening around a large *Pholidophorus*, masks familiar deformational features, such as the marginal sulcus (note centrifugal foresetting!) and the collapse caldera. The lack of an adequate lower caldera and the bowl shape of the compressed body suggest that concretionary processes had started below the carcass before the major collapse. The slight upward deflection of lower layers may express either a preceding pedestal, or a caldera reduced by concretionary stiffening of the sediment, GPIT 1489/26.

B.-D. Ammonites (and smaller fishes) lack the concretionary modification. Their asymmetry is in the opposite direction (pedestal; lower caldera deeper than the upper) and more than compensates for the possible difference in level between the median plane of the shell and the surface on which it came to rest. Sections through the aperture (upper blocks) show the underthrusting of the apertural plug underneath the apertural depression. Note that drusy calcite (hatched) within the shells has not visibly modified the collapse (secondary recrystallization?). For bedding plane views of D and B see Figs. 10 and 12. GPIT 1489/27-29.

criteria for a two stage collapse. One of them is a calcite crust in the phragmocone section, cut off, as it seems, along the last septum. Closer examination reveals that the calcite often extends into the body chamber as a narrow tongue along the umbilical shoulder (Fig. 9), and sometimes also along the keel, i. e. along the rigid zones that had resisted the body chamber collapse (Fig. 2). The extension into the phragmocone, however, is inconsistent with the concept of a drusy calcite filling the empty chambers: Instead of the expected segmental arrangement we find a puddle-like outline of the calcite crust.



Fig. 9. In accordance with the two-phase collapse, shell fractures are restricted to the body chambers (phragmocone cracks in A are septarian, while drusy calcite (shaded) is restricted to spaces that remained open after the body chamber collapse (phragmocone behind the telescope fracture; area of umbilical and keel fractures; see Fig. 2). Fracture patterns are largely determined by the apertural plug and the inner whorl. Note also that the phosphatic siphuncle in A is sediment-covered only in the apertural plug.

GPIT 1489/30-36 (B same as SEILACHER, in press, Fig. 11, B).

Therefore we suggest that the calcite has formed in spaces that remained open after the body chamber collapse and after the septa separating the chambers had disappeared ("hollow phragmocone stage" Fig. 18, A). Very likely the phragmocone collapsed less suddenly than the body chamber, with the collapse starting in the thin-shelled inner whorls and gradually continuing towards the telescope fracture.

c) Collapse calderas:

For preservational studies it is of particular importance that compaction in the lithographic limestones did not continue indefinitely after the shells had collapsed. It is difficult to tell exactly when the cementation occurred, but almost without exception it was after the shell collapse and still early enough to preserve deformational structures on adjacent bedding planes above and below the fossils, which are not found in more shaly sediments. In this group of phenomena, the pedestal preservation ("Sockel-Erhaltung") of Solnhofen fossils is the most familiar. But it has detracted the attention from the collapse features which we shall discuss before, because they throw new light also on the explanation of the pedestals.

On adjacent bedding planes one observes shallow depressions that differ from the pedestal in having opposite relief above and below the ammonite (Fig. 10). As they always deflect towards the ammonite, correspond to its outline, and are shallower over the umbilicus, there can be no doubt that they represent collapse calderas (JANICKE 1969, VAN STRAATEN 1971). Like other collapse features they are not geopetal, indicating an origin under considerable sediment cover.

It was most interesting to discover that the two-stage collapse of Oppelia is also expressed in the shape of the caldera: Not only is the phragmocone caldera deeper than that of the body chamber, but it is also labelled by sharper outlines marked by minute antithetic faults. Both differences indicate a more advanced stage of compaction by the time of the phragmocone collapse: The sediment was not only stiffer, reacting by microfaults rather than deflection, but the phragmocone caldera also had less chance to flatten out by subsequent compaction or by lateral adjustment through sediment flow.

d) Marginal sulcus:

As we have mentioned, the collapse calderas are in principle non-geopetal structures. In specimens from Nusplingen (Fig. 7, C) and from calcareous beds of the Upper Posidonia Shales (Fig. 19, C) it is in fact impossible to distinguish the lower from the upper caldera. In Solnhofen ammonites however, the upper caldera differs from the lower by a rim, or sulcus, that contours the spiral of the last whorl. Its repetition at higher levels and an interruption across the aperture indicate that it cannot be simply material squeezed out by the sinking shell. Its outer slope is soft, i.e. without the micro-faults seen in the phragmocone caldera.

Cross sections reveal that we are not dealing with a deformational feature, but with a sedimentary wedge that has piled up against the walls

of the ammonite venter (Fig. 8) and got widened by foresetting before it became gradually levelled-out in higher laminae.

The marginal sulcus seems to indicate a very special mode of sedimentation: A normal current would have eroded directional scour marks around the obstacle, or accumulated sediment on the downcurrent side. In contrast, a rain of fine particles in completely quiet water would have



Fig. 10. Bedding plane views of specimen Fig. 8, D. Note the difference between lower (A) and upper calderas (C, D). The stronger convexity in the lower phragmocone caldera reflects the drusy calcite in the shell. Wintershof b. Eichstärt; GPIT 1489/29.

Preservational history of compressed Jurassic ammonites

coated the shell with sheets of fairly constant thickness. What we actually observe reflects a state of non-directional turbulence that might have developed in the final phase of a density current in the limited Solnhofen basins.

e) Pedestal:

The "Sockel-Erhaltung", i.e. the fact that fossils themselves appear elevated above the surrounding bedding surface and that — in contrast to stylolitic phenomena — corresponding elevations can be traced into over- and underlying bedding planes, is a well known phenomenon in the Solnhofen limestones. It has long been used to recognize upper and lower sides in museum specimens.

Similar pedestals are found in the Middle Triassic lithographic shales of Montral, Spain (HEMLEBEN, in preparation), but they are absent in the more shaly "Fäulen" layers in Solnhofen and in other known lithographic limestones.

After having singled out the other preservational elements that are usually associated, it will be easier to discuss the various explanations that have been previously suggested for the Solnhofen pedestals:

• Buoyancy by gases that developed during temporary emersion in decaying shells or carcasses glued to a sticky mud flat surface (ROTH-PLETZ, 1910; ABEL, 1927): This explanation is physically objectable. It becomes obsolete with the rejection of the mud flat model (BARTHEL, 1964).

• Buoyancy of water-filled shells enclosed in soupy mud (BARTHEL, 1964; JANICKE, 1969): This mechanism, comparable to rock salt diapirism, could have become effective as the mud gradually densified. Shells with largely sediment-filled body chambers should be expected to tilt during this process. In the case of *Oppelia* shells, diapirism should have also continued for the phragmocone part after the body chamber had collapsed. Instead, we observe a uniform pedestal level throughout the shell. It would also be difficult to understand why pedestals are equally developed in shrimps and fishes (whose flexible carcasses have certainly collapsed before the ammonite shells), unless the diapirism was early.

• Concretionary carbonate concentration around the fossil (STRUNZ, 1928; MAYR, 1966): Since fossils tend to maintain a position above the center of the concretion (Fig. 16, A), subsequent compaction would produce a pedestal. Such concretionary pedestals have in fact been observed in Solnhofen reptiles (STRUNZ, 1928) and larger fishes (Fig. 8, A). This model can not be applied, however, to ammonite and small fish pedestals, which flatten out in deeper levels without becoming inverted (Fig. 8, B—C).

• Shell collapse within the sediment (VAN STRAATEN, 1971): This explanation is supported by the fact that pedestals occur only in collapsable bodies such as ammonite shells, squids, shrimps or fishes, but never in isolated shell fragments, belemnite rostra, or aptychi (Fig. 15). It may also account for some geopetal asymmetry, i. e. that the collapsing fossil appears elevated: If the shell had not sunk into the underlying mud, its neutral plane remained at a higher level, resulting in an upward collapse of the lower shell impression. However, JANICKE, Pl. 7, Fig. 1) has described a *Perisphinctes* specimen, in which the outer whorl is not collapsed; nevertheless the layers above and below do show an upward pedestal deformation. On the other hand, specimens from Nusplingen (Fig. 7, C) and from the Posidonia Shales (Fig. 19, C) show that the collpase itself may be quite symmetrical, without any sign of a pedestal.

In conclusion, none of the proposed single mechanisms sufficiently explains all pedestal phenomena. Obviously, we deal with a rather complex feature in which sedimentational (sulcus), compactional (calderas), cementational (concretion) and perhaps diapiric processes in an unusual sediment are involved. In order to single them out, it will be necessary to carefully study a still larger number of specimens and different fossil groups in vertical and serial sections.

f) Level of shell solution:

The question, how deep in the sediment the dissolution occurred, is to some extent answered by the following observation: In the Solnhofen section, slumping is recorded by small scale folding and overthrusting in several horizons ("krumme Lagen"; Fig. 11, A), which are used as regional date lines. Most slumped units are in the order of 1-2 m thick. Fallen blocks from one of these horizons contain flattened Oppelia shells, whose siphuncular spirals have become latterally compressed in the slump direction which can be derived from associated slip planes (Fig. 11, C). Since the shells did not fracture, they had already dissolved before the slumping occurred, that is in less than 2 m depth (measured in the compacted state).

Results:

- 1. With regard to ammonite preservation, lithographic limestones closely resemble the bituminous shales. This means that cementational processes did not start until compaction had been largely completed.
- 2. The marginal sulcus around the shell and its upper calderas suggests burial in a state of nondirectional turbulence, as may occur in the final phase of turbidity currents in small basins.
- 3. Collapse calderas and apertural plug confirm the two-stage collapse for Oppelia and indicate a rather coherent sediment that was deposited fast enough to produce analogous preservational features also in soft bodies of fish and squids.

328

- 4. Puddles of drusy calcite have formed after the collapse of the body chamber, probably during the "hollow phragmocone" stage.
- 5. Because of its complexity, the pedestal around the shell can not yet be attributed to any single process.
- 6. The shells became dissolved in the upper few meters of sediment, while the mud was still soft enough to slump.

B. Lytoceras type

Shells of this group have no keel; still they resemble the oxycone shells of the *Harpoceras* type in a mechanical sense: Disc-shaped enough to be deposited in a horizontal position, they have a wide body chamber that is not corrugated enough to resist compactional forces. Accordingly, we find again a two-phase collapse. Its effects are even more obvious here than in the *Harpoceras* type, because the sherds of the breaking body chamber are not being hold together by a resistant keel ring. As a result, the sherds tend to be scattered and to protrude beyond the spiral contour, producing a much more rugged outline than in the *Harpoceras* type.



Fig. 11. Fractureless lateral deformation of *Oppelia* impressions (C) by synsedimentary slumping indicates that shell solution occurred in the upper few meters of sediment. Since the slab was collected from float, it is not clear whether it actually came from the slump-folded "Krumme Lage" (A, from FESEFELDT 1962) nor whether the elongation was in slump direction (tensional deformation in proximal area) or at right angles to it (compressional deformation in distal slump).

Note that after optical transformation into undeformed spirals (B) the slip planes from a rectangular grit.

Horst Quarry, Solnhofen; GPIT 1489/37. (B, C from SEILACHER, in press).

1. Lytoceras in the Opalinus Clay

Two species of *Lytoceras* are found at different levels in the Mössingen section:

- (a) At a lower level, *L. torulosum* is associated with beer mat *Leioceras* and shows the same compressional features. These include the telescope fracture passing into an umbilical fracture (Fig. 3, C), but with more irregular fractures around the perimeter.
- (b) L. lineatum occurs at the level in which Leioceras is preserved with body chamber concretions and presents the same preservation (Fig. 17).
- 2. Phylloceras and Lytoceras in the Posidonia Shales

Lytoceras and Phylloceras shells grow considerably larger than Harpoceras in this unit. This may be the reason why their body chambers have collapsed even earlier, with the angular sherds protruding beyond the spiral outline (Fig. 6). Sculptural details are very well preserved in these sherds (Fig. 5, B).

Nevertheless, all shell parts became eventually dissolved, leaving only the conellae (HÖLDER & MOSEBACH, 1950), which in *Lytoceras* may be distributed over the whole body chamber wall. The perfect preservation of the conellae, with their pointed tips always pointing to the outer shell surface, suggests that they had already been calcitic by the time of burial. Whether this was due either to localized calcitic biomineralization or to very early diagenetic alterations in the aragonitic shell layer (BANDEL & HEMLEBEN, 1975) remains an open question.

The phragmocone, in sharp contrast to the body chamber, has lost its sculptural details, but preserves the perfect spiral outline through softfoil collapse (therefore only the phragmocone is being cut out by the quarrymen for decorative purposes).

In one Lytoceras specimen (GPIT 1489/56), the entire apertural ring lies undeformed at the side of the crushed body chamber. Since this delicate structure could impossibly have survived the collapse and become tilted within the sediment without breakage, it is supposed that it became detached before burial. Similar rings have also been found isolated without associated shells. Thus we suppose that they became actively shed off before the conotheca continued to grow after a stadial phase.

The other possibility, that the whole body chamber broke before being buried in the sediment, can be excluded: Implosion would affect the phragmocone rather than the body chamber, while predators would have hardly crushed the shell, in all cases, right to the last septum and left all the fragments together.

Results:

- 1. Non-keeled, involute ammonites with a fairly high whorl section suffered a twostage collapse similar to the *Harpoceras* type.
- 2. Differences in fracture pattern are explained by the lack of a keel that hold the spreading fragments together in the *Harpoceras* type.

C. Dactylioceras type

In this type we group rather evolute shells, whose tube-like conotheca was reinforced by strong radial corrugations (*Perisphinctes*), or hollow ribs (*Dactylioceras*), which made them much more resistant against compressional deformation than the *Harpoceras* and *Phylloceras* types of shells. The phragmocone, on the other hand, was designed for r a dial butressing and therefore weaker against the lateral compactional stress than in the *Harpoceras* type. As a result, there was no two-phase collapse, i. e. the body chamber has collapsed more or less simultaneously with the phragmocone, after the shell had lost most of its original rigidity. This gives us an opportunity to countercheck preservational features in those rocks, in which *Dactylioceras*-like shells occur together with geometrically different types, for instance in the Posidonia Shales and in the Solnhofen lithographic limestones.

1. Dactylioceras in the Posidonia Shales

Since this is one of the most common ammonites in the Posidonia shales, there is no lack of observational data.

Specimens in the shale never show any sign of a two-phase collapse (Fig. 5, C). Neither telescope fractures, nor different modes of fracturing in the body chamber versus the phragmocone have been observed. It is true that the collapse was not always fractureless; but, in contrast to the *Lytoceras* type, the outline remains always a smooth spiral in spite of the fact that there was not keel to catch the fragments. Therefore we use the term "entire leaf preservation" in analogy to the "partial leaf preservation" in *Harpoceras*.

2. Perisphinctes in the Solnhofen limestones

If we consider, in terms of general geometry, *Perisphinctes* (and the rare *Hybonoticeras*) as an analogue to *Dactylioceras*, we may again expect supplementary evidence from the Solnhofen type of preservation.

a) Collapse caldera and pedestal:

The shape of the collapse caldera confirms a uniform and relatively late event: Both underneath and above the persphinctid shell the caldera is a single depression including the phragmocone and the body chamber section. Its contour is never soft like in the body chamber caldera of Oppelia, but marked throughout by minute faultlines (Fig. 12). This indicates that the collapse has happened in the stiff-mud stage and was approximately contemporaneous with the collapse of the Oppelia phragmocone.



Fig. 12 (Legend see p. 333)

Corresponding to the wider whorl, the caldera tends to be deeper than in *Oppelia* and can therefore be traced through relatively greater thicknesses below and above the shell. In successive layers, the radius of the caldera may slightly decrease away from the shell, due to synthetic inclination of the collapse faults, which in broken specimens may also appear slickensided.

Pedestals are pronounced; but it should be noted that they are also present along calcite-filled body chambers (Figs. 8, B and 13).

Corresponding to the broader venter, the marginal sulcus (Fig. 12) is also higher than in *Oppelia*. As the diameter of this sulcus increases through foresetting, its contours become more clearly separated from the narrowing caldera in the higher laminae.

b) Apertural plug, depression and avalanche:

The apertural plug is present in most specimens. In contrast to *Oppelia*, it may extend far into the body chamber (Fig. 13, A). Or it is a short wedge bounded by the circular caldera and therefore broader on the ventral than on the dorsal side of the aperture (Fig. 13, B-E).

As might be expected in a wider shell that remained open for a longer time, the a pertural depression is more pronounced than in *Oppelia* and can be traced to a higher level above the shell (Figs. 12, 13). Cross sections reveal, that this depression not only compensates for the bulging of the sulcus, but actually reduces the thickness of the laminae involved. They also show the underthrust of layers that we have noted in *Oppelia* (Fig. 8). This detail may be understood in connection with another feature that we did not observe in *Oppelia*: In the bedding plane containing the shell, a set of fine concentric fault lines around the aperture marks the displacement of already stiff sediment into the open body chamber. This "a pertural alvalanche" (Fig. 12, e) is situated not only below the apertural depression itself, but extends into the body chamber, consistent with an oblique displacement of sediment down into the aperture.

Fig. 12. Successive bedding plane views of *Perisphinctes* Fig. 8, B before sectioning. The whole caldera is microfaulted, suggesting a one-phase collapse contemporaneous with the phragmocone collapse in *Oppelia* (Fig. 7 and 10). The upper caldera (f) differs from the ones underneath the shell (a-d) by marginal sulcus and apertural depression (with concentric microfaults). It also has a higher umbilical hump, indicating that the lower unbilicus was not sediment-filled. This also explains the slight downward depression of the collapsed umbilicus in most shells. Note that the drusy calcite has influenced only the lower calcera (b-d; see also Fig. 10), and more so on the left side, where the calcite body is larger than on the opposite side of the last whorl (Fig. 8, B). GPIT 1489/28.

The view that the apertural plug, depression and avalanche are expressions of the same process is also corroborated by the fact that they are found in the same combination around accidental holes in the body chamber wall (SEILACHER, in press, Fig. 11, C).

While actually released by sediment pressure, the plug formation may be described as suction exerted by the open aperture. It is interesting to note that this "suction" was not symmetrical. Apertural depressions have never been found on underlying laminae, probably because the sediment was already stiffer there than in the upper layers. A relatively steep compactional gradient is also indicated by the difference between avalanche and overlying depression: Although it resembles the avalanche in relief and dimension and is only a few millimeters above, the depression never



Fig. 13. In contrast to *Oppelia* (Fig. 9) the drusy calcite of *Perisphinctes* shells (shaded) is restricted to the proximal part of the last whorl (except for the narrow backward extension in A, corresponding to the spiral fracture); but it is not reflected in the upper caldera. Note the collapse-deformed landing mark in A. GPIT 1489/38-42.

shows microfaulting. We have not yet been able to determine how deep in the sediment the apertural depression has actually formed, but probably it was no more than a few centimeters.

c) Drusy calcite fillings:

The calcite puddle of *Oppelia* also has an interesting counterpart in *Perisphinctes*. In both forms it tends to be absent in softer, less calcareous layers. It also has the same granular appearance failing to express finer details of the shell ornamentation; but it differs completely in position: In *Oppelia*, the calcite has formed in the phragmocone (with narrow marginal extensions into the body chamber). In *Perisphinctes*, calcite is restricted to the body chamber (which in this genus is somewhat longer than the last whorl), while the phragmocone contains neither calcite nor sediment and has thus become completely flattened.

Provided all calcite puddles are essentially contemporaneous, their occurrence in the Perisphinetes body chamber, which remained open well into the hollow ammonite stage, is not surprising. But it is hard to explain why in this form the calcite does not extend into the phragmocone.

One could argue that — like in Oppelia — the thinner wall of the inner whorls was dissolved first. Along with the solution, the collapse would then gradually proceed along the spiral. In contrast to Oppelia, however, the collapse would not stop at the end of the phragmocone but rather at the point where the load of the outer whorl ceased with the end of the umbilical suture.

While this problem remains unsolved for the moment, the high relief of the *Perisphinctes* shell allows to study the behaviour of the calcite body during the collapse in more detail than in *Oppelia*.

As usual in Solnhofen fossils (p. 323), only the lower surface of the calcite bcdy is exposed on bedding planes (Fig. 12). It preserves the undeformed wall curvature in a general way as if it had been a solid calcite filling of the entire body chamber cavity. In fact, the collapse calderas below such shells, instead of showing maximum depression along the cuter whorl, contour the calcitized parts in convex forms, while the phragmocone calderas are more deeply impressed and form the usual umbilical elevation in the center (Fig. 12). A bove the calcitized body chamber, however, the collapse caldera is no different from an uncalcitized shell: It shows a deep depression extending throughout the phragmocone caldera and the body chamber section (Fig. 12, 13); only the sediment plugs press through, causing the collapse caldera to shallow near the aperture.

This deviation from the usual non-geopetal collapse indicates (1) that the calcite has filled only a small part of the body chamber cavity, (2) that it lined — in contrast to geopetal void fillings — mainly the lower wall and reinforced it against the subsequent collapse deformation, and (3) that it may have grown by recrystallization after the collapse.

Geopetal druses may occur and seem to be a normal feature also in ammonite cavities of the Lower Triassic bituminous shales of Southern Switzerland (RIEBER, 1973, p. 12). Another possibility would be that the drusy calcite lining was originally uniform, but disintegrated with the solution of the aragonite wall. The crystal debris could then have accumulated at the bottom of the residual cavity and welded enough to reinforce this part during the final collapse.

It should also be noted that the larger calcite bodies in *Perisphinctes* often have a hollow center, in spite of the fact that they were not formed as druses in the undeformed body chamber cavity. We suspect that this is an effect of later recrystallization.

Results:

- 1. In agreement with their shell geometry, *Dactylioceras* in the Posidonia Shales as well as *Persphinctes* (and *Hybonoticeras*) from Solnhofen lack signs of a two phase collapse.
- 2. In Solnhofen perisphinctid shells, the form of the caldera also confirms that the body chamber has suffered a late, one-phase collapse together with the phragmocone. Before this collapse, compaction had time to press the sediment farther into the body chamber, producing an apertural plug with avalanche structures in the shell level and a deep, but softer apertural depression in higher levels.
- 3. In this case, drusy calcite has formed in the body chamber rather than in the phragmocone, selectively reinforcing the lower wall during the final collapse.

D. Aspidoceras type

We mention this type for completeness, although it is represented only in some of the rocks studied and only by a small number of specimens. With regard to shell statics, *Aspidoceras* would be classified with the *Lytoceras* type. Because of the broad venter (often accentuated by marginal spines), however, *Aspidoceras* type shells often came to rest in vertical position resulting in particular types of compactional deformation.

1. Nautilus from the Posidonia Shales

In previous faunal lists of the Posidonia Shales, *Nautilus* does not appear, although it is common in other zones of the German Lias. Two specimens found in recent years (courtesy of GOTTHILF and JÜRGEN FISCHER, Holzmaden) suggest that this was partly an observational bias: Both specimens are embedded in a vertical position and with the body chambers so badly broken, that little similarity is left with the original *Nautilus* shell (Fig. 5, D).

This discovery is particularly interesting, not only because of its biological implications, but also in view of recent studies about the implosion and deposition of modern *Nautilus* shells. According to experiments and

336



Fig. 14. Sections through Aspidoceras shells buried in their vertical landing position (see Fig. 5, D) suggest compaction of the Solnhofen mud to 1/6-1/9 of its original volume. Fracture lines in the body chamber wall, soft deformation around the body chamber and microfaulting of the phragmocone caldera suggest a two-phase collapse. A secondary anticlockwise rotation is indicated by deflected layers in both specimens. GPIT 1489/43-44.

calculations with empty shells (RAUP, 1973; WEAVER & CHAMBERLAIN, 1976), Nautilus could not become vertically imbedded at depths beyond 7—10 m. This limit would not apply, however, for shells with intact siphuncular tube that become more slowly water-filled and change to horizontal sinking position at much greater depth. The vertical position could be preserved, if the shells become buried immediately after having reached the bottom. Exception should also be made for shells that sank with the soft body in place, which is no improbable situation for the Posidonia Shales as well as the Solnhofen Limestones.

Both Holzmaden specimens indicate a two phase collapse, in which only the body chamber became broken, while the phragmocone survived until a later soft foil collapse.

2. Aspidoceras from the lithographic limestones

In Solnhofen as well as in Nusplingen, the majority of the Aspidoceras shells is also preserved in upright position and compressed to an almost unrecognizable elliptical shape. The true extent of flattening is revealed by vertical sections (Fig. 14), which show that the volume of the calderas is an order of magnitude smaller than the volume of the collapsed shell This misproportion can only be explained by an extreme degree of compaction of the whole sediment to about 1/6 to 1/8 of its original volume. Nevertheless we observe microfaulted caldera contours on top (and presumably below) the phragmocone section only. This indicates that both collapse phases happened during the early part of compaction. It is also interesting to compare the pedestal situation with horizontally imbedded shells. While it seems to be true that the net collapse is larger upward than downward, the apical side of the lower contour is bending the beds downward in contrast to the upward bend on the apertural side. This indicates a relative rotation of the leading edges in the vertical plane during the collapse.

In one specimen (Fig. 15) the heavy aptychus has fallen out of the body chamber, letting the shell tilt to an oblique position. In this case only the shell has a pedestal. On the other hand the weight of the soft body can not alone be responsible for the vertical orientation, since many of the vertically embedded *Aspidoceras* lack an aptychus.



Fig. 15. Aspidoceras shell that sank into an oblique position after the heavy aptychi had fallen out of the aperture. Note that a pedestal (A) and a corresponding upper caldera has formed only around the shell, not around the massive aptychus. (Thickness of layer: 12 mm) GPIT 1489/45.

Results:

- 1. In the Posidonia Shales and the Solnhofen Limestones, shells with a broad venter (*Nautilus, Aspidoceras, Waagenoceras*) predominantly maintained their vertical landing positions.
- 2. In agreement with their shell geometry, they suffered a two-phase collapse.
- 3. Both collapses happened early in the compaction phase, which eventually reduced the sediment to 1/6 to 1/9 of its original thickness in the Solnhofen case.

III. Modification by concretionary processes

Calcareous concretions are the product of early diagenetic differentiation. By studying their relationship to ammonite preservation, we may hope to differentiate the cementational processes involved and to correlate them with our relative time scale of ammonite diagenesis. During the course of this study it became evident, that the Posidonia Shales are particularly rich in concretionary phenomena and that the interbedded bituminous limestone horizons, not usually considered as concretions, should also be included.

A. Isolated concretions

In contrast to concretions in sands and silts, which tend to be spheroidal, shale concretions are usually flattened due to the greater permeability parallel, than at right angle, to the bedding plane. This effect is more pronounced the more the sediment had been compacted before. Subsequent compaction has often accentuated their contour by onion-skinning shale laminae around the flanks of the concretions.

1. Nucleus concretions:

The simplest relationship goes along with the wide-spread assumption that the decay of soft parts has triggered the local precipitation of carbonate from saturated pore fluids. Accordingly, the fossil, or rather the originally most fleshy parts of it, should be in the center of the concretion.

Such "nucleus concretions" are found at certain horizons within the Posidonia Shales around larger vertebrate skeletons or squids. They deviate slightly from the general scheme in the following details:

- The fossil tends to be above the median plane of the concretion.
- Marginal parts of the body often protrude laterally.
- Concretions smaller than several decimeters across are practically absent.

As a consequence, nucleus concretions are found only around larger carcasses, such as ichthyosaurs, large fishes (*Lepidotus*, Fig. 16, A), large squids, or drift wood with thick *Inoceramus* overgrowth. In these, the halo of scattered *Lepidotus* scales, or the whole skeleton around the concretion below an ichthyosaur stomach are often pressed down by compaction since they lie above the center of the concretion.

This agrees with the concretionary thickening of beds in Solnhofen, which is also restricted to the larger vertebrates (Fig. 8, A; STRUNZ, 1928).

Surprisingly, individual nucleus concretions have never been found around Posidonia shale ammonites, which are among the most common fossils and often reach diameters of about 40 cm. Perhaps the ammonite



Fig. 16 (Legend see p. 341)

soft body did not reach the critical mass to trigger the concretionary process; or it had, lacking strong muscles, been disintegrated earlier than other carcasses.

In less extreme environments, like the Lias shales of Whitby (England) ammonite nucleus concretions do occur in all sizes. Enclosed shells of *Phylloceras* have the body chamber collapsed with telescope fracture, indicating that the concretion had formed at some depth in the sediment, probably long after the decay of the soft parts.

In our South German material, ammonitic nucleus concretions occur cnly at certain horizons of the Opalinus Clay; but they usually contain several specimens. In this case the shell surfaces are often coated with a veneer of spathic calcite, which seems to have formed in septartian shrinkage clefts (compare HOLLMANN, 1968 and our Fig. 1, C).

2. Accidental inclusions:

Considering how rich the Posidonia Shales are in ammonites, one should expect many cases in which these had become accidentally enclosed into larger concretions. Still only two such cases have so far been called to our attention.

The first case was reported to us by JÜRGEN FISCHER (Holzmaden). It is the concretionary envelope of an ichthyosaur skeleton which preserves on its lower surface the umbilical impression of a larger *Harpoceras* (Fig. 16, F), and encloses, between the ribs and vertebrae, many small shells of *Dactylioceras* (up to 2 cm in diameter) in a perfectly undeformed state. Unlike all other Posidonia Shale ammonites, the enclosed shells preserve, between the clear calcite of the chamber fillings, the shell wall and the septa as a white and probably still aragonitic substance. This case is

Fig. 16. In the Posidonia Shales, like in the Solnhofen limestones (Fig. 8, A) nucleus concretions occur only around large squids, fish and reptiles (A). Ammonites, if at all, have formed concretions (B-E) which preserve an undeformed cast only of the umbilical face. Shell parts beyond the "umbilical watershed" (white areas in plane views) remained clear from the concretion, but became pressed onto it after the shell was reduced to a flexible foil at a later stage (arrows). Note that the pyrite halo (shaded in vertical sections) reaches the surface only along the original contact with the shell. While typical umbilicus concretions are known only with *Hildaites* of the upper Posidonia shales (B-E) and only from float specimens, a similar preservation is observed in a *Harpoceras* from a lower level that happened to lie close to an idthyosaur nucleus concretion (F). In this case, position of the shell below the concretion has been observed in the field (J. FISCHER, personal communication) and early cementation is attested by undeformed aragonitic *Dactylioceras* shells within the concretion.

- A. Lepidotus; Dotternhausen; GPIT 1489/46.
- B-E. Hildaites; Holzheim; Staatl. Museum f. Naturkunde, Stuttgart.
- F. Harpoceras; Holzmaden; GPIT 1489/47.

important because it shows (1) that concretions did, in special cases, form before the solution of aragonitic shells and (2) that the shells did — in contrast to the present situation in the Baltic Sea (LEWY, 1975) — not dissolve at the surface, but only after they had been buried in the sediment.

The second case is a large, flat concretion (ϕ 50 cm; GPIT 1489/57) from Dotternhausen. In contrast to other concretions it is less calcified, being still fissile, and without sharp boundaries. It contains the calcitic shells of *Inoceramus* undeformed, but *Dactylioceras* shells dissolved and flattened except for the sediment-filled body chambers, which still preserve some of their convexity either on the upper or lower flank. It has obviously been cemented in a later phase, similar to the bituminous limestone beds (Gelbe Platte and *Inoceramus* Bed) discussed in a later paragraph.

3. Umbilicus concretions (Fig. 16, C-F):

Half a dozen specimens of *Hildaites* singled out by the late F. BERCK-HEMER in the Stuttgart Museum (Staatl. Museum für Naturkunde) drew our attention to a very remarkable type of preservation. These specimens, including an additional one recently found by FRITZ SAUTER (Aalen; GPIT 1489/58), all come from the uppermost part of the Posidonia shales, but from widely separated localities.

Here, in contrast to the nucleus concretions, the shell is not enclosed into the concretion, but has left an external imprint — as if the concretion had been pressed against the ammonite like a ball of modelling clay. In the central, i.e. umbilical part, this impression is completely undeformed and preserves all sculptural details, including growth lines. The marginal parts of the shell, however, appear pressed down over the slopes of the concretion like the soft brim of a felt hat. The lack of fractures and the lcss of sculptural details indicates that this deformation has happened at a later stage, after the shell had been dissolved and collapsed to a flexible periostracum foil.

Highly polished sections show that the laminae inside are parallel to each other and are only in the marginal zone deflected towards the neutral midline of the concretion. In some specimens, the shell, lying somewhat off the vertical axis of the concretion, has caused an asymmetrical hump. As a result, the midline happens to be at different levels on oposite sides, so that some of the laminae became deformed into a sigmoidal shape (Fig. 16, D and F).

The sections also reveal that the pyritic halo around the center, which should properly be concentric (EINSELE & MOSEBACH 1955, p. 364), reaches the surface of the concretion at the side of the ammonite, but only along its undeformed umbilical impression (Fig. 16).

342

Even our limited material leaves little doubt that, like in the nucleus type and in the *Amaltheus* concretions described earlier, we deal with an early phase of cementation, whose association with the ammonites is not purely accidental. But by what effect has the ammonite shell triggered, or at least influenced, the growth of the concretion? One clue lies probably in the pyrite distribution and in the fact that the undeformed impression, i. e. the primary contact with the concretion, is restricted to the umbilical concavity: Like the concave valves of *Plagiostoma* in the Lower Lias, or the concave carapaces of Eocene crabs (MUNDLOS, 1975), the umbilicus seems to have acted as a shield that blocked and concentrated the diffusion of the concretionary process.

The assumption that the shells have modified, rather than triggered, the concretionary process is corroborated not only by the excentricity of some specimens, but also by the fact that the ichthyosaur concretion containing undeformed *Dactylioceras* (Fig. 16, F) shows the umbilical impression of a larger *Harpoceras* shell with all the described features on its surface. Thus it is a general phenomenon that may also occur at other levels and with other ammonite genera involved.

This shield effect is likely to be geopetal. F. BERCKHEMER noted in a label that in his specimens the impression is on the upper side of the concretion. But in the Dewangen specimen (GPIT 1489/58) it could be shown by geopetal voids, and in the ichthyosaur concretion by in situ observations, that the shells were on the lower sides. More evidence is obviously needed before this question can be settled. Future research on this line might also include the phosphatic concretionary pillows found in the umbilical area of ammonites in other shales (p. 313).

It should be mentioned that in the Dewangen concretion several smaller and completely undeformed ammonites are also enclosed. In addition, the master shell is closer to the concretion's median level and its body chamber has remained undeformed. This indicates a combination with the effects that we are going to discuss in the following chapter.

4. Pressure shadow concretions in body chambers:

In Leioceras from a level above the beer mat ammonites in the Mössingen section, and from many other localities, only the phragmocone appears collapsed in the "beer mat" fashion, while the body chamber preserves its original geometry (Fig. 17). The traditional explanation would be that the fill sediment of the body chamber became hardened previous to the collapse by concretionary cementation, and that this process was triggered by the decomposition of ammonite soft parts. But a few significant details do not fit this model:

1. In contrast to other concretions (for instance pyritic ones), the cementation never extends outside the shell; it does not even reach the aperture, which appears squeezed together by subsequent compaction in a *Phragmoceras* fashion.

- 2. On the upper side, the body chamber wall is often fractured by collapse into a void running along the crest of the sedimentary fill.
- 3. Except for the void collapse, the cemented body chambers appear completely undeformed and never "exploded".

The same criteria apply to the Muschelkalk ceratites (SEILACHER, 1971) except for the fact that their sediment fill and its concretionary cementation extends well into the phragmocone. In this case, however, subsequent shell and periostracum solution has eliminated other types of preservation, while pressure solution may have later produced double suture lines and changed the geometry of the surviving ceratite steinkerns.



Fig. 17. Body chamber concretions from the Opalinus Clay always end short of the aperture, indicating preferential cementation of the fill sediment in the pressure shadow of the shell. The concretion saved the body chamber from compactional deformation except for the compression of the aperture and local collapse into voids of the fill sediment (top views, A and C; geopetal structure). The empty phragmocone collapsed like usual (Fig. 3).

Association with a different species of *Lytoceras* indicates that this preservation is restricted to a higher stratigraphic level in the Mössingen section.

- A-B. Leioceras; GPIT 1489/48-49.
- C. Lytoceras lineatum; GPIT 1489/50.

Although it produces a similar end product, the cementational process under consideration seems to basically differ from the accretionary growth of true concretions (SEIBOLD, 1962): In the pressure shadow of the shell, the fill sediment maintained its pore space and thereby favored the precipitation of cementing minerals during the compaction of the surrounding sediment. It is by the same principle that the sedimentary fills of burrows dug into precompacted sediments, or the rigid frameworks of coquina layers and shell "nests", have become selectively cemented.

Like the nucleus and shield concretions, pressure shadow concretions represent a very early generation of cementational processes. None of the three has been found in ammonites of the lower, most bituminous part of the Posidonia Shales, except for the one ichthyosaur concretion. The Lower Lias (Sinemurian) of Southern Germany also contains, at slightly varying levels, local seams of dark bituminous shales which allow comparison with the preservational features observed in the Posidonia Shales. With respect to ammonites, only Dactylioceras types of shells are represented. Accordingly, they appear flattened in a one-phase collapse; but their body chamber fill sometimes appears lighter-colored than bedrock and phragmocone, at least in fresh specimens. Chemical analysis (U. HÜCKEL, personal communication; GPIT 1489/59) shows that this is due to a slightly higher carbonate content $(27,8 \text{ versus } 21^{\circ}/_{\circ})$ in the body chamber fill than in the rest of the shale. We mention this as an intermediate case, in which pressure shadow concentration did act, but was too weak to protect the shell from compactional flattening.

Results:

- 1. While ammonitic nucleus concretions do occur in other dark shales and in certain horizons of the Opalinus Clay, they are never found in the Posidonia Shales (or in Solnhofen) — not even around very large shells.
- 2. Only ammonite shells accidentally enclosed in vertebrate nucleus concretions were affected by this early form of cementation.
- 3. Larger ammonites could influence concretionary cementation in the adjacent sediment through the shield effect of their umbilicus.
- 4. In the pressure shadow inside the body chamber, sediment could also become preferentially cemented, reinforcing this part of the shell against compactional collapse.

B. Bituminous limestone beds

Large concretions occur scattered throughout the Posidonia Shales; but the occurrence of many concretions without larger fossils, and of complete vertebrate skeletons without concretions, indicates that they represent certain levels with a higher cementation potential.

In addition, there is a number of bituminous limestone beds, of which the lower three can be traced over a distance of more than 100 km along the strike. In weathered sections, each of these beds can be recognized by



Fig. 18. Ammonites from bituminous Limestone beds within the Posidonia Shales.

- A. "Hollow phragmocone" preservation of *Dactylioceras* in the "Laibstein" horizon (Holzmaden) suggests very early cementation followed by aragonite solution. Note that the drusy calcite shows no trace of the septa but covers the phosphatic siphuncle (from ANDALIB, 1971).
- B. Flattened *Harpoceras* with phragmocone dome on top of the Inoceramus Bed (Dotternhausen; GPIT 1489/51; compare Fig. 19, A). Same specimen as SEI-LACHER, in press, Fig. 13, C.
- C. "Half ammonite" from inside the same bed. Cementation occured after shell solution and after the phragmocone collapse, but before the fill sediment of the collapsed body chamber was completely compacted, thus preserving the telescope

characteristic features: The lowermost rhythmically changes in thickness so that it appears like a mosaic of bread loaves ("Laibstein-Bank"); the next is poorly laminated and weathers with a yellow tint ("Gelbe Platte"); the third is very uniform in thickness and finely laminated ("Oberer Stein"). In addition, we will discuss a bed, about 2 m above the "Oberer Stein", which is developed only in the Dotternhausen area and characterized by a basal layer of *Inoceramus* shells ("Inoceramus-Bank").

Except for the "Laibstein-Bank" these beds seem to represent the episodic deposition of a more calcareous ooze, for instance by coccolithic blooms. The occurrence of faunal elements (for instance Leptolepis) and of sedimentary structures (roll marks of fish vertebrae and other faint tool marks), unknown from the surrounding shales, seems to support this view. But the occurrence of sudden thinnings suggests that concretionary processes have also been involved in the formation of these seemingly uniform beds.

A geochemical survey by U. REINKENSMEIER (personal coummunication) has shown that there is an upward decrease of the carbonate content, not only within the indvidual beds, but also from bed to bed. This is interesting, as the ammonite preservation indicates a more and more retarded cementation in the same sequence.

1. Hollow-phragmocone preservation:

The "Laibstein-Bank" contains many minute gastropods (Coelodiscus) in an uncompressed, calcite-filled state of preservation. Larger ammonites are rare, and only Dactylioceras has so far been found. They are preserved as "hollow ammonites" (Fig. 18, A), i. e. they have a continuous drusy coating of brown bituminous calcite throughout the open phragmocone. There are no indications of septa any more, but the phosphatic tube of the siphuncle is still in place (ANDALIB, 1971). In a way, we deal with a similar preservation as in the famous "Altdorf marble" (marginal facies of similar age farther East), only that the drusy calcite has proceeded to completely fill the phragmocones in the Altdorf Dactylioceras shells.

Both cases may be compared to the "hollow ammonite" stage with dissolved septa that has been postulated for the shell collapse in earlier chapters. In the case of the Laibstein ammonites, septal solution seems to have occurred after the cementation of the surrounding sediment (it affects the shell wall as well as the septa), but certainly before the onset of drusy

fracture better than in shale specimens (Fig. 5, A). For section of the same specimen see Fig. 19, B; GPIT 1489/52.

D. Hildaites from a micro-coquina in the Upper Posidonia Shales; Wutach area. In agreement with its *Dactylioceras*-like geometry, the shell suffered only one collapse phase, during which the sediment-filled body chamber remained undeformed. Compare sections of same specimen in Fig. 19, C; GPIT 1489/53.





Fig. 19 (Legend see p. 349)

calcite growth. This is the main difference from the undeformed, but shell bearing ammonites found in nucleus concretions (Fig. 16, F), which also represent a very early phase of cementation.

2. Half-ammonite preservation:

Harpoceras shells in the "Gelbe Platte" and the "Inoceramus Bank" more closely resemble the shale preservation, in that they have flattened phragmocones. The body chamber, however, appears hardly deformed, in spite of having lost its shell and showing an uncompressed telescope fracture at the rear end (Figs. 18, C and 19, B). Upon closer inspection it becomes obvious that only the lower flanks of the body chambers are preserved in this way and that their upper halves can neither be split open nor be detected in vertical sections.

One might the tempted to explain this phenomenon by mechanical corrosion or subsolution (HOLLMANN, 1962) from above.

A specimen of *Hildaites* from a more calcareous microcoquina bed of the Posidonia shales (Fig. 18, C—D), as well as similarly preserved ammonites from dolomitic layers in Lower Triassic bituminous shales of Southern Switzerland (RIEBER, 1973, Fig. 3), disprove this explanation: A caldera above the body chamber, similar to the ones observed in Solnhofen *Perisphinctes* (Fig. 13), clearly indicates that the upper half has been lost after burial through diagenetic solution. The geopetality of this solution may be explained by partial sedimentary filling, which sealed the lower part of the body chamber, while the upper remained more accessible. It is by the same principle that the completely non-sealed septa were the first parts of the shell to become dissolved.

Fig. 19. Ammonites from Posidonia Shale limestone beds, cross-sectioned.

- A. Harpoceras with phragmocone dome; top of Inoceramus Bed, Dotternhausen (compare similar specimen in Fig. 18, B). — Carbonate/clay ratios, computed from more detailed analyses by H. PUCHELT, are highest in the central level of the bed (lower block). Laterally, they are uniform in overlying shale, but significantly higher underneath the elevated phragmocone than below the depressed body chamber. This suggests concretionary growth of the limestone bed within fairly compacted mud. Note low ratio of the body chamber fill, in contrast to the situation in the earlier body chamber concretions (Fig. 17). GPIT 1489/54.
- B. Half-ammonite specimen of same species, but from within the same bed (same specimen as Fig. 18, C), has no phragmocone dome. It also lacks the roof part of the body chamber. Since the body chamber collapse proceeded as usual, and since the roof is present in shale specimens (A, and Fig. 5, A), its loss is considered as a later event related to cementation.
- C. Cross sections through specimen Fig. 18, D reveal a similar situation, while bedding plane deformations (tentatively traced from debris orientation and colour bands) suggest that the body chamber roof got lost before the phragmocone collapse, which is compensated at a higher elevel. In contrast to the Solnhofen pedestal preservation (Fig. 8, B) layers are deformed symmetrically above and below the shell.

Significantly, isolated sherds of ammonite walls do not follow this rule: They may be convex-down as well as convex-up in the same bed. Unfortunately, *Dactylioceras* shells have not yet been found in either of the two beds; we would expect them to show the same preservation.

3. Completely flattened shells:

In the "Oberer Stein", ammonite preservation indicates that the sediment became cemented at a still later stage in the compactional sequence: Its *Harpoceras* shells are almost as flat as the ones in the shales. The only difference is a yellowish, spathic veneer (siderite ?) in the phragmocone section. We tend to compare it to the calcite puddle in Solnhofen *Oppelia*. In this sense it could indicate the onset of calcite formation in the hollow phragmocones before the final collapse, related to an already higher carbonate content of the original sediment.

4. Phragmocone domes:

In the "Gelbe Platte", as well as in the "Inoceramus-Bank", the halfammonite preservation of *Harpoceras* in side the limestone goes along with a very peculiar preservation of the same genus on top of the bed, where the limestone grades into shale. Here, the phragmocones show an upward convexity, which has nothing to do with the original curvature of the shell wall: Not only are the spiral depressions of the umbilical seams missing, but the umbilicus itself is bulging up, and the phosphatic siphuncle, often zig-zagged by the previous phragmocone collapse, is deformed into a low helicoidal spiral (Fig. 18, B).

We clearly deal with a secondary compactional deformation of an already flattened periostracal leaf over an underlying calcification center. However, in contrast to the umbilical shield and other concretions of the earlier generation, this center does not form an individualized body, but a protrusion of the underlying gradational limestone surface. In agreement with this interpretation, smaller shells have the dome only in close proximity to the bed, while a few millimeters higher only the larger shells show this phenomenon.

Chemical analyses carried out by H. PUCHELT (personal communication) in fact show consistent increase of carbonate under the dome compared to the lateral extension of the same laminae (Fig. 19, A). In both profiles the carbonate ratio is highest in the median level, which agrees with the assumed concretionary character and growth of this limestone bed. Also of interest is the low carbonate content in the compressed fill sediment of the body chamber, in contrast to the situation in body chamber concretions. Why, however, did only the phragmocone, and not the body chamber section of the already flattened shell, "attract" the cementation front? The difference may be related to the different compactional histories of the two parts: The body chamber not only contained some sediment, but also broke into sherds rather than collapsing as a complete periostracal shcet. But even the largest body chamber fragments are never individually domed. Therefore we tend to believe that the difference was related to shell structure. Like *Oppelia* in Solnhofen and aragonitic ammonites in other localities (BAYER, 1975), *Harpoceras* in the Posidonia Shales shows indications of a thin phosphatic lining of the phragmocone chambers, particularly under ultraviolet light (ANDALIB, 1971, Fig. 7). It would go along with its presumed blotting-paper function in the living animal that this layer did continue to act as a special sheet during diagenesis, making the cementation front of the underlying limestone bed advance faster underneath the phragmocones of the already flattened shell leaves.

A similar phragmecone dome also occurs in *Phylloceras* (GPIT 1489/60) from the same level, but unfortunately no *Dactylioceras* has as yet been found in this situation.

5. Preservation in coquina layers:

In the concretions and bituminous limestone beds discussed so far, the crigin of the carbonate cement remains uncertain. EINSELE & MOSEBACH (1955, p. 376) concluded that it was directly precipitated from the sea water. The discovery of abundant coccoliths (G. MÜLLER & BLASCHKE, 1969; GRÜN, 1974) in the Posidonia Shales has introduced another possible source. The coccoliths may at the same time explain diagenetic similarities with the Solnhofen limestones, which are also highly coccolithic (FLÜGEL, 1967). Since coccolith ooze is calcitic, this carbonate became mobilized only at a later stage of diagenesis, after the aragonitic shells had already been dissolved and flattened.

A different preservational situation might be expected in the microcoquina layers occurring at various levels in the Posidonia Shales. Here the great number of wholly or partly aragonitic shells should have provided carbonate cement at an earlier stage. The most prominent of these layers ("Schlacke") is well developed at Holzmaden, where it also contains large amounts of phosphatic fish debris and belemnite rostra. These show weakly preferred orientation, imposed by a basinward current from SE to NW (H. D. BERGNER, personal communication, 1974; BRENNER, 1975). In spite of the abundant shell material present, ammonite preservation in the Schlacke is little different from the purer shales: The shells are completely flattened, only that they became irregularly buckled during compaction of the less homogeneous sediment. This unexpected result may be explained, however. In large-scale horizontal and vertical sections now on exhibit in the Tübingen museum, the ammonite body chambers can be recognized by their fill sediment which is considerably finer than the sediment outside the shell. This situation indicates a secondary increase in turbulence. The current that winnowed the fines except inside the ammonite shells, may also have brought more shell debris from other areas. This debris may have been considerably older than the ammonites and had possibly lost most of its aragonite during early diagenesis in its primary site of deposition.

Like in the other limestone beds of the Posidonia Shales, preservation is not the same in all coquina horizons. The half ammonite described earlier (Figs. 18, D and 19, C) represents a case of earlier cementation.

We should also mention a case in which a coquina layer did modify the course of fossilisation in another way. A loose slab discovered by F. LÖRCHER in the Dotternhausen quarry (replicas GPIT 1489/61) shows radial calcitic veins that by their mode of branching remind septarian cracks. But closer examination reveals that they originated from the septa of an ammonite. Although the original orientation remains unknown, there is little doubt that carbonate from an adjacent thin coquina layer has entered the septal fissures before they became closed after the shell solution.

Results:

- 1. Ammonite preservation in different bituminous limestone beds of the Posidonia Shales reveals considerable differences in the mode and time of cementation.
- 2. Early cementation of the "Laibsteinbank" prevented collapse of the shells, but not their transformation into hollow ammonites by later shell solution and subsequent drusy lining. It also accounts for the irregular thickness of the bed.
- 3. In the "Gelbe Platte" and the "Inoceramus Bank", cementation post-dated the solution and the collapse of the ammonite shells, but the fully sediment-scaled shell parts and isolated sherds remained relatively undeformed.
- 4. Upward concretionary growth of these two beds is indicated by the phragmocone doming of already flattened shale ammonites that happened to lie near the cementation front.
- 5. Completely flattened ammonites in the "Oberer Stein" indicate still later cementation, which is also responsible for the uniform thickness of this bed.
- 6. Flattened ammonites in the "Schlacken" suggest that the enclosing shell debris was largely calcitic, probably due to aragonite solution at a previous site of deposition, while other coquina horizons show other cementation histories.

IV. Concluding remarks

Preservational features are not random, but can be analyzed and typified according to the principles of morphology. Nor are they randomly distributed, but correlate with rock types, without simply duplicating lithologic classifications. This seems to us the most encouraging result of this pilot study.

Fossilization, however, is not an independent field. The biological characteristics of the fossilized objects and their post-mortem sedimenta-

tional history must be understood before their diagenetic history can be successfully analyzed. Also, geochemical analyses should properly complement the morphological approach. This calls for integrated research, involving paleobiologists as well as sedimentologists and geochemists and covering the whole spectrum of preservational regimes as well as later diagenetic processes that are not necessarily expressed by deformational features.



Fig. 20. Tentative flow diagram of observed preservational stages (excluding pedestals, pyritisation and half ammonites).

- (1) Unaltered shell (preserved by early cementation; see Fig. 16, F).
- (2) Hollow phragmocone stage (hypothetical).
- (3) Periostracum foil, undeformed (Laibstein-Bed of Posid. Sh.).
- (4) Body chamber collapsed with telescope fracture (stage preserved in pyritized specimens, Amalth. Sh.).
- (5) Beer mat preservation after second collapse phase (some pyritized specimens in Amaltheus Sh.; Opalinus Clay).
- (6) Partial leaf preservation (Posid. Sh., lithogr. ls.).
- (7) Entire leaf preservation of *Dactylioceras* type (Posid. Sh., lithogr. ls.).
- (8) Nucleus concretion (Posid. Sh., in connection with large vertebrate carcasses; Opalinus Clay). May also contain stage 4.
- (9) Body chamber concretion (Amalth. Sh.; Opalinus Clay).
- (10) Umbilicus concretion (Posid. Sh.; orientation should possibly be inverted).
- (11) Phragmocone dome (top of Gelbe Platte and Inoceramus Bed in Posid. Sh.).

From SEILACHER (in press).

The present study falls short of these requirements in several respects. The main preservational phenomena observed can, nevertheless, be synthesized in a flow diagram (Fig. 20), which expresses the general time sequence of diagenetic events and processes in the given sample. Many more formations and other groups of fossils need to be studied in similar detail, before a comprehensive classification of preservational facies can be proposed. Such studies will not only reveal many new features but also cases that are intermediate between the types described in this paper. Still we are confident that this approach will stand future tests and that fossils can be used as field tools not only in a biostratigraphic, but also in a petrogenetic sense.

References

- ABEL, O.: Lebensbilder aus der Tierwelt der Vorzeit. 714 S., Gustav Fischer, Jena 1927.
- ANDALIB, F.: Mineralogisch-geochemische Untersuchungen der aragonitischen Fossilien aus dem Dogger alpha (Opalinuston) in Württemberg. — Arb. Geol.-Paläont. Inst. Stuttgart, N. F., 62, Stuttgart 1970.
 - Mineralogy and preservation of siphuncles in Jurassic cephalopods. N. Jb. Geol. Paläont. Abh., 140: 33–48, Stuttgart 1972.
 - Erhaltung von Aragonitschalen im Dogger alpha (unteres Aalenium) Südwestdeutschlands. - Geol. Rdsch., 62: 506-521, Stuttgart 1973.
- BANDEL, K. & HEMLEBEN, C.: Anorganisches Kristallwachstum bei lebenden Mollusken. — Paläont. Z., 49: 298—320, Stuttgart 1975.
- BARTHEL, K. W.: Zur Entstehung der Solnhofener Plattenkalke (unteres Untertithon). — Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 4: 37—69, München 1964.
- BAYER, U.: Die Runzelschicht ein Leichtbauelement der Ammonitenschale. Paläont. Z., 48: 6—15, Stuttgart 1974.
 - Organische Tapeten im Ammoniten-Phragmokon und ihr Einfluß auf die Fossilisation. – N. Jb. Geol. Paläont., Mh. 1975, 12–25, Stuttgart 1975.
- BRENNER, K.: Ammoniten-Gehäuse als Anzeiger von Palaeo-Strömungen. N. Jb. Geol. Paläont. Abh., 151: 101–118, Stuttgart 1976.
- EINSELE, G. & MOSEBACH, R.: Zur Petrographie, Fossilerhaltung und Entstehung der Gesteine des Posidonienschiefers im schwäbischen Jura. — N. Jb. Geol. Paläont. Abh., 101: Stuttgart 1955.
- FESEFELDT, K.: Schichtenfolge und Lagerung des oberen Weißjura zwischen Solnhofen und der Donau (Südl. Frankenalb). — Erlanger Geol. Abh., 46: 1—80, Erlangen 1962.
- FLÜGEL, E. & FRANZ, H. E.: Elektronenmikroskopischer Nachweis von Coccolithen im Solnhofener Plattenkalk (Oberjura). — N. Jb. Geol. Paläont., Abh., 127: 245—263, Stuttgart 1967.
- GROISS, J. TH.: Mikropaläontologische Untersuchung der Solnhofener Schichten im Gebiet um Eichstätt (südliche Frankenalb). — Erlanger geol. Abh., 66: 75— 93, Erlangen 1967.
- GRÜN, W., PRINS, P. & ZWEILI, F.: Coccolithophoriden aus dem Lias epsilon von Holzmaden (Deutschland). — N. Jb. Geol. Paläont. Abh., 147, 294—328, Stuttgart 1974.

- HENGSBACH, R.: Ein Harpoceras aus dem Posidonienschiefer mit erhaltener Lobenlinie. — Der Aufschluß, 25: 465—466, 1974.
- HÖLDER, H. & MOSEBACH, R.: Die Conellen auf Ammonitensteinkernen als Schalenrelikte fossiler Cephalopoden. — N. Jb. Geol. Paläont. Abh., 92: 367—414, Stuttgart 1950.
- HEMLEBEN, C.: Fossillagerstätten in plattigen Kalken: Zbl. Geol. Paläont. II, 1976: 214–222.
- HOLLMANN, R.: Über die Subsolution und die "Knollenkalke" des Calcare Ammonitico Rosso Superiore im Monte Baldo (Malm, Norditalien). — N. Jb. Geol. Paläont., Mh. 1962: 1963—1979, Stuttgart 1962.
 - Diagenetische Gehäuse-Hypertrophie an Ammoniten aus dem Oberjura Ostafrikas. – N. Jb. Geol. Paläont., Abh. 130: 305–334, Stuttgart 1968.
- HUDSON, J. D. & PALFRAMAN, D. F. B.: The ecology and preservation of the Oxford Clay fauna at Woodham, Buckinghamshire. — Quart. J. Geol. Soc. London, 124: 387—418, London 1969.
- JANICKE, V.: Untersuchungen über den Biotop der Solnhofener Plattenkalke. Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 9: 117—181, München 1969 (Dissertation 1967).
- LEWY, Z.: Early diagenesis of calcareous skeletons in the Baltic Sea, Western Germany. — Meyniana, 27: 29–33, Kiel 1975.
- MAYR, F. X.: Zur Frage des "Auftriebes" und der Einbettung bei Fossilien der Solnhofener Schichten. — Geol. Bl. NO-Bayern, 16: 102–107, Erlangen 1966.
- MÜLLER, G. & BLASCHKE, R.: Zur Entstehung des Posidonienschiefers (Lias ε). Naturwissenschaften, 56: 635, Heidelberg 1969.
- MUNDLOS, R.: Ökologie, Biotratinomie und Diagenese brachyurer Krebse aus dem Alt-Tertiär von Helmstedt (Niedersachsen, BRD). — N. Jb. Geol. Paläont. Abh., 148: 252–271, Stuttgart 1975.
- NEUMANN, N. & SCHUMANN, D.: Zur Fossilerhaltung, besonders der Goniatiten, in roten Knollenkalken vom "Ammonitico-Rosso"-Typ. — N. Jb. Geol. Paläont., Mh. 1974: 294—314, Stuttgart 1974.
- RIEBER, H.: Cephalopoden aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kanton Tessin, Schweiz). — Schweiz. Paläont. Abh., 93: 1—96, Basel 1973.
- ROTHPLEZ, A.: Über die Einbettung der Ammoniten in die Solnhofener Schichten. Abh. Kgl. Bayer. Akad. Wiss., 2. Kl., 24: 313 ff, München 1909.
- SCHINDEWOLF, O. H.: Über Aptychen (Ammonoidea). Palaeontographica, A, 111: 1—46, Stuttgart 1958.
- SEIBOLD, E.: Kalk-Konkretionen und karbonatisch gebundenes Magnesium. Geochimica Cosmochimica Acta, 26: 899—909, 1962.
- SEILACHER, A.: Preservational history of Ceratite shells. Palaeontology, 14: 16— 21, London 1971.
 - Mechanische Simulation und funktionelle Evolution des Ammoniten-Septums.
 Paläont. Z., 49: 268–286, Stuttgart 1975.
 - Post-mortem history of Ammonites. In: MOORE (ed.): Treatise on Invertebrate Paleontology, Part L, revised edition (in press).
- STRAATEN, L. M. J. U. VAN: Origin of Solnhofen limestone. Geol. en Mijnbouw., 50: 3-8, 1971.
- STRUNZ, CHR.: Aus der Werkstatt des Präparators. 2. Die Präparation eines Pleurosaurus-Skeletts. — Natur u. Museum, 58. Ber. Senckenberg. Naturf. Ges., S. 116—121, Frankfurt a. M. 1928.

356 A. Seilacher, F. Andalib, G. Dietl and G. Gocht, Preservational history

- RAUP, D. M.: Depth inferences from vertically imbedded cephalopods. Lethaia, 6: 217—226, Uppsala 1973.
- VEIZER, J.: Geochemistry of lithographic limestones and dark marls from the Jurassic of Southern Germany. N. Jb. Geol. Paläont., Abh. (in press).
- WEAVER, J. S. & CHAMERLAIN, J. A.: Equations of motion for post-mortem sinking of cephalopod shells and the sinking of *Nautilus*. — Paleobiology, 2: 8—18, 1976.

Anschriften der Verfasser:

Prof. Dr. A. SEILACHER, Dr. H. GOCHT, Geol. Paläont. Institut Tübingen, Sigwartstraße 10, 7400 Tübingen 1; Dipl.-Geol. G. DIETL, Staatl. Museum für Naturkunde, Arsenalplatz 3, 7141 Ludwigsburg; Dr. F. ANDALIB, P. O. Box 1964, Teheran/Iran.