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Ammonite ecology in Late Jurassic time in northern Switzerland

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Key words: Ammonites, Late Jurassic, fossilization, taphonomy, paleoecology

ABSTRACT

This paper is based on 221 detailed stratigraphical sections and 11 major bed by bed excavations for macrofossils that were done from 1961 to 1995 between Boncourt JU in northwestern Switzerland and Möhringen on the Danube in southern Germany. Four variables of sedimentation were reconstructed in the central Jura, in Canton Aargau and in Canton Schaffhausen. It can be read from these diagrams that the optimal habitat of ammonites was in water deeper than about 50 m. Ammonites or their prey could tolerate only a very low average sedimentation rate which was much lower than that tolerated by certain hermatypic corals like platy microsolenids. Ammonites could adapt to a low oxygen content in the water: The minimum content was of the order of 1ml/l or about 20% of the normal level.

ZUSAMMENFASSUNG

Die vorliegende Arbeit ist auf 221 stratigraphischen Detailprofilen und 11 grösseren systematischen Grabungen nach Makrofossilien gegründet, welche von 1961 bis 1995 zwischen Boncourt JU in der Nordwestschweiz und Möhringen and der Donau in Süddeutschland ausgeführt worden sind. Vier Variabeln der Sedimentation wurden rekonstruiert im zentralen Jura, im Kanton Aargau und im Kanton Schaffhausen. Aus diesen Diagrammen geht hervor, dass der optimale Lebensraum der Ammoniten sich in einer Wassertiefe von mehr als etwa 50 m befand. Ammoniten oder ihre Beute konnten nur eine sehr geringe durchschnittliche Sedimentationsgeschwindigkeit ertragen, welche weit unter derjenigen lag, die gewisse hermatypische Korallen wie tellerförmige Microsoleniden aushielten. Ammoniten konnten sich an einen niedrigen Sauerstoffgehalt des Wassers anpassen: Der Minimalgehalt lag in der Grössenordnung von 1ml/l oder etwa 20 % des normalen Gehaltes.

Introduction

221 detailed stratigraphical sections of the Late Jurassic were measured between 1961 and 1995 in northern Switzerland and adjacent southern Germany. The most important of these were published by Gygi (1966, 1969, 1977), Gygi et al. (1979), Gygi & Marchand (1982) and Gygi (1990a, 1999a). 11 large scale systematic excavations for macrofossils were made between 1970 and 1991 in especially rich strata from the upper Callovian to the Kimmeridgian in northern Switzerland (tab. 1). The coordinates of the excavations are given in Gygi (1999a, tab. 1). The sections of the excavations are published in Gygi (1977), Gygi et al. (1979), Gygi & Marchand (1982) and Gygi (1990a, b). About 9000 ammonites have been found in situ in the excavations. The excavated strata have been dated radiometrically by Gygi & McDowell (1970) and Fischer & Gygi (1989).

The purpose of this paper is to evaluate previously published data and to draw conclusions of the abundance of fossilized ammonites and the influence of the sedimentation rate, the water depth and the oxygen content of the bottom water on the fossilization frequency of ammonites. The full names of the bio-and lithostratigraphic units shown in Figs. 1–3 are given in Gygi (1999a). For the time-stratigraphic position of the lithostratigraphic units see tab. 2 in Gygi & Persoz (1986) and Gygi (1999a, fig. 40).

Methods

Ammonite abundance: The number of entirely fossilized ammonites per excavated fossiliferous rock volume can be calculated by dividing the number of ammonites through the rock volume. The volumes of excavated rock were read from the excavation reports in the field books of the author, and the number of ammonites in a given stratum was counted in the collection.

Sedimentation rate: The rate of sedimentation was calculated from the averaged thicknesses of the lithostratigraphic

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Tab. 1. Location and lithostratigraphical range of the large-scale systematic excavations for macrofossils made in northern Switzerland.

RG	51b	Oberehrendingen AG: Birmenstorf Mb.-Effingen Mb.
RG	70	Mellikon AG: Crenularis Mb. - Baden Mb.
RG	81b	Gächlingen SH: Herznach Fm. - Effingen Mb.
RG	207	Siblingen SH, Wasserleitung: Herznach Fm. - Effingen Mb.
RG	208	Üken AG: Herznach Fm. - Birmenstorf Mb.
RG	212	Siblingen SH, Schiessstand: Herznach Fm. - Effingen Mb.
RG	225	Gansingen AG, Eisengraben: Birmenstorf Mb.
RG	230	Gansingen AG, north of Eisengraben: Birmenstorf Mb.
RG	239	Schaffhausen, Summerhalde: Wangental Mb. - Schwarzbach Fm.
RG	276	Holderbank AG, Chalch quarry: Varians Mb. - Effingen Mb.
RG	280	Liesberg BL, Ampthil: Herznach Fm. - Renggeri Mb.

units as published mainly by Gygi (1999a, fig. 39). These calculations are based on the assumption that the ammonite subzones were of equal duration. Radiometric ages are taken from the latest Jurassic time scale by Gradstein et al. (1995).

Water depth: Water depths in the Late Jurassic of northern Switzerland have been concluded by Gygi (1981) based on sedimentological, taphonomical and mineralogical evidence. The good correlation within the Late Jurassic platform to basin transition in northern Switzerland and the fact that part of the basin was completely filled with sediments in the northwest made calculations of water depths possible on the assumption that regional endogenic (thermal) subsidence was equable (Gygi 1986) in all of northern Switzerland. The curves of water depth in Figs. 1–3 were drawn disregarding sequence stratigraphy (see Gygi et al. 1998). The following corrections of the data given in Gygi (1986) can be made: The initial water depth in northwestern Switzerland was at most 60 m. The relative sea level rise in the Oxfordian Age in northern Switzerland was 120 m. Consequently, the water depth near Schaffhausen at the end of the Oxfordian was about 140 m, not 120 m as was calculated by Gygi (1986, p. 472).

Oxygen content of the bottom water: It can be concluded from the taphonomy of ammonites that the oxygen content of the bottom water varied between aerobic and dysaeorobic. The water was never anaerobic for an extended time (Gygi 1969, p. 107). The figures of oxygen content given in Figs. 1–3 are based on published data. Byers (1977, p. 7) stated that the oxygen content in marine surface water is normally about 7ml dissolved O_2 per liter of water in temperate climates. The paleolatitude of northern Switzerland was about 33° N in the Late Jurassic (Smith et al. 1981, maps 34 and 38), and the tropical and subtropical belts were at that time wider than today (Beauvais 1977). At least subtropical temperatures must therefore be assumed for sea water at the surface in northern Switzerland in Late Jurassic time. Consequently, a maximum of 5ml dissolved oxygen per liter of bottom water is estimated in Figs. 1–3, because the oxygen saturation diminishes with risig temperature, and oxygen is consumed by organisms with depth (Richards 1957, tabs. 4–5, fig. 7). The 5ml O_2/l of the bottom water in the northwestern Gulf of Mexico given in fig. 11 by Richards (1957) are the closest Recent counterpart to the Late Jurassic of northen Switzerland that could be found in the literature.

Results

The results of the calculations of ammonite abundance, sedimentation rate and water depth as well as the estimates of oxygen content of the bottom water are presented in Fig. 1 for the Central Jura, in Fig. 2 for Canton Aargau and in Fig. 3 for Canton Schaffhausen.

Discussion

1. Central Jura (Fig. 1)

Ammonite abundance: Ammonites are very abundant and prevail in the macrofauna at the boundary between the Middle and Upper Jurassic (upper Herznach Formation). It is impossible to give an exact figure of the abundance in this bed, because there is a transition between incomplete and complete preservation of ammonites. The small maximum in the lower Renggeri Member is that recorded in excavation RG 280 in the clay pit of Ampthil near Liesberg BL. The ammonites in the Renggeri Member are preserved as steinkerns of iron sulfide (pyrite and marcasite, represented by a bold line in Figs. 1-3).The peak in the Sornetan Member (Gygi 1999a, olim: Terrain à Chailles) occurs only in the distal part of this member, in the „fossil bed“ of Gygi & Persoz (1986, tab. 2). Ammonites prevail in the macrofauna of this bed. Further up in the succession, ammonites are rare to the extent that it is difficult to date sediments biostratigraphically (Gygi 1995).

Sedimentation rate: The rate of sedimentation was minimal at the beginning of the Oxfordian. Then it became normal. There is no sedimentological evidence that the rate dropped at the time when ammonites were relatively abundant in the lower Renggeri Member (excavation RG 280, Liesberg BL, 2m above the base of the member). The mean sedimentation rate of the Renggeri Member is 0.5m/10'000a. According to Brett & Baird (1986, p. 217), this is at the lower limit of the typical sedimentation rate interval for iron sulfide steinkern formation. The sharp drop of the sedimentation rate in the fossil bed in the middle of the Sornetan Member (Fig. 1) is presumed because of the sea level rise that Gygi (1986, fig. 4) concluded at the end of the Cordatum Subchron. None of the ammonites excavated from in situ was encrusted by serpulids or showed other evidence of starved sedimentation. The peak of the sedimentation rate of the Liesberg Member refers to section RG 306 in the Chestel clay pit near Liesberg BL, the type locality of the member, where the thickness of the Liesberg Member is with 25m about twice as much as in other sections. A high percentage of the mud of the Liesberg Member was argillaceous. The heavy siliciclastic sediment input did not prevent the growth of hermatypic corals. In fact, the corals (mainly microsolenids) make up as much as 30% of the rock volume of the Liesberg Member at the type locality.

Water depth: The depth of the water at the beginning of the Oxfordian in the Central Jura cannot be established precisely. The order of magnitude is adapted from P.A. Ziegler (1982, p. 106) who stated that about 3000 m of sediments can

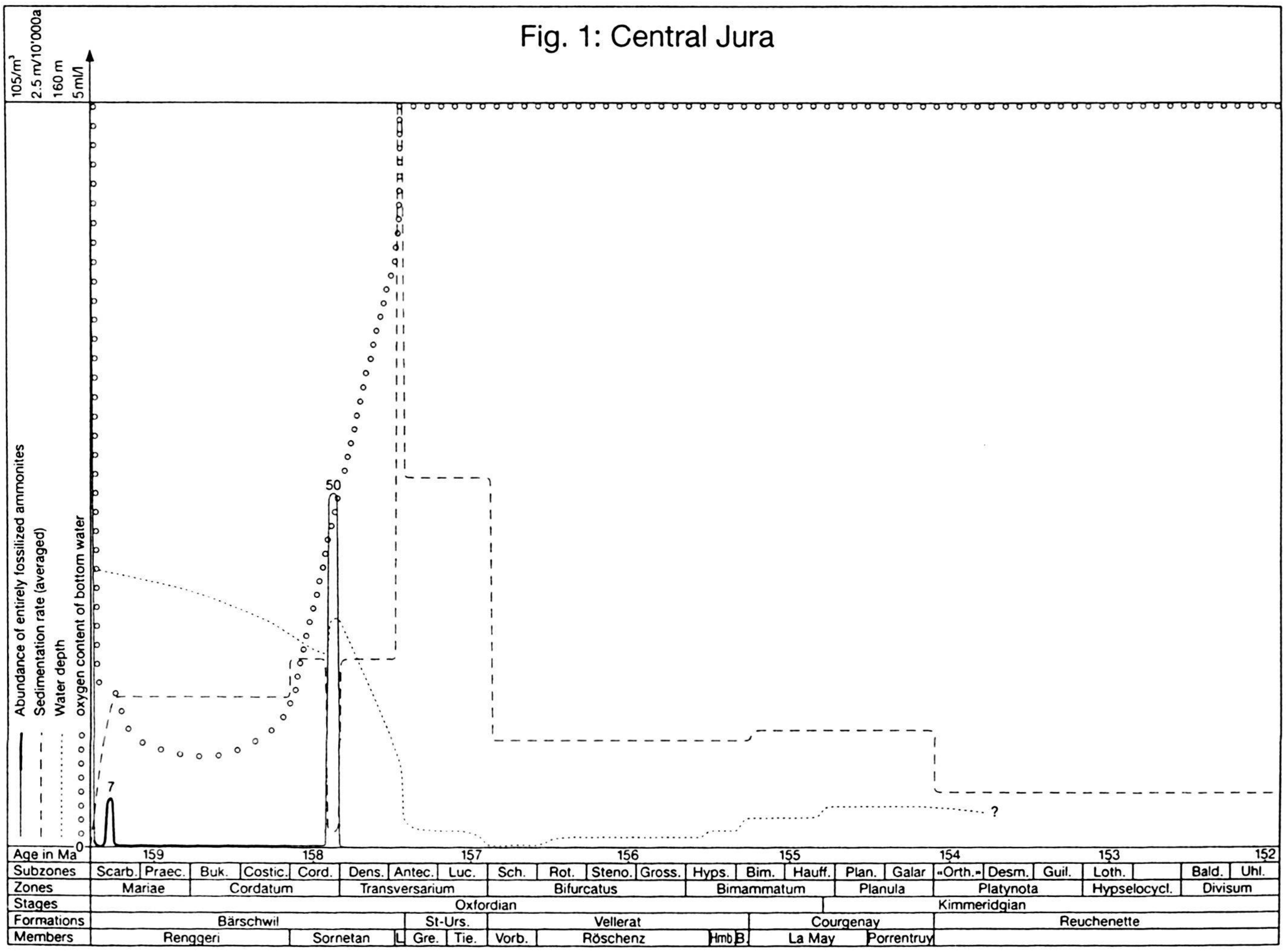

Fig. 1. Variables of sedimentation in the central Jura. The scales of the curves are given in the upper left corner of Figs. 1–3. The curves of ammonite abundance are represented as a bold line where ammonites are fossilized as steinkerns of iron sulfide.

accumulate in a basin with an initial water depth of 1000 m. Gygi (1986, p. 470) wrote that the averaged and compacted thickness of sediments from the beginning of the Oxfordian to the end of the Transversarium Chron was in the Central Jura 185m, and that the basin was completely filled up by the end of that time. The initial depth of the basin must then have been at least 60 m at the beginning of the Oxfordian, if no endogenic subsidence and eustatic sea level rise occurred. But endogenic (thermal) subsidence and eustatic sea level rise very probably did occur at this time (Gygi 1986). 60 m water depth at the beginning of the Oxfordian in the Central Jura are then to be considered as a maximum. A falling tendency of sea level during the early Oxfordian and a rise at the end of the Cordatum Subchron was inferred based on evidence from dinoflagellates by Ghasemi in Ghasemi et al. (1999). The depth interval of 60-80 m as was inferred by Insalaco (1996, p. 183) for microsolenid biostromes like in the Liesberg Member seems to be much too great in the case of the Liesberg Member which is overlain by bioarenitic-oncolitic packstone and oolite near Liesberg (section RG 306, pl. 31 in Gygi 1999a). During the sedimentation of the Röschenz Member, the sediment surface got temporarily into the supratidal zone (M.A Ziegler 1962, p. 42, Gygi 1992, figs. 5–6).

Oxygen content of bottom water: The bottom water was normally oxygenated at the beginning of the Oxfordian in the Central Jura. This is documented by the limonitic, iron oolitic marl-clay with a rich, cephalopod-dominated macrofauna at the top of the Herznach Formation which is a regional marker bed that was deposited at a low sedimentation rate. At the beginning of the sedimentation of the Renggeri Member, the sedimentation rate increased and with it the supply of siliciclastic mud from land. The latter must have brought about the input

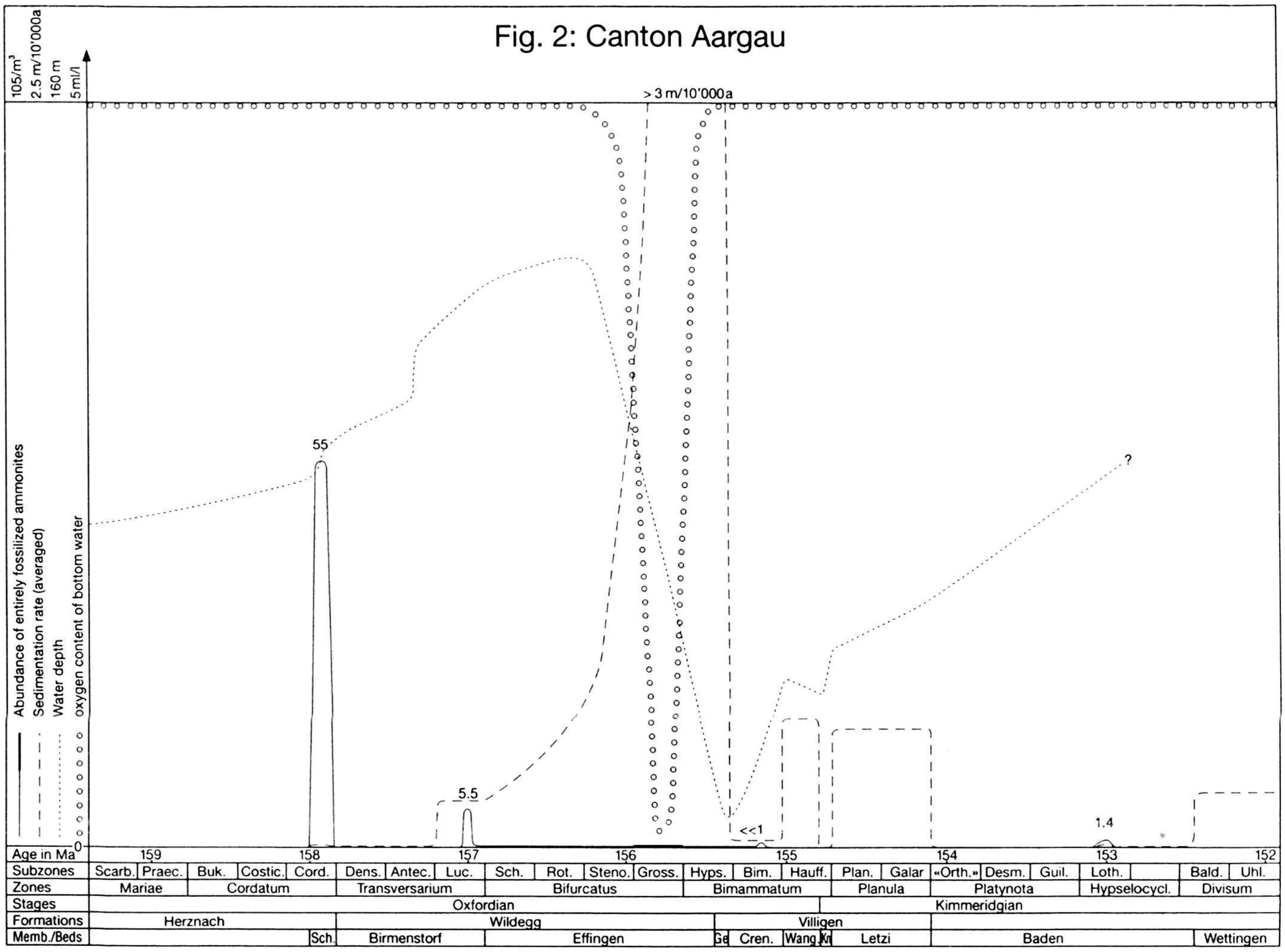

Fig. 2. Variables of sedimentation in Canton Aargau.

of organic matter to the basin. Decomposition of the organic matter consumed much of the oxygen in the water. Because of this, the oxygen content of the bottom water must have sharply dropped. The macrofauna of the Renggeri Member is dominated by ammonites, but there are also rare sessile organisms like brachiopods and bivalves. The maximum diameter of the ammonites is about 3cm, but most of them are smaller. The majority of them is preserved with part of the body chamber. The ammonites are then dwarfed. All of them are preserved as casts of iron sulfide where the Renggeri Member has a normal thickness. The iron sulfide was formed during early diagenesis, because the body chamber of some of the larger ammonites is sometimes flattened by the later compaction of the sediment where the body chamber contains no iron sulfide. The inner whorls with a high sulfide content are not compressed. The sediment is burrowed. This is another indication that the bottom water was not anoxic. But the diameter of the burrows is always small. It is seldom more than 1mm (Gygi 1999a, fig. 6). According to Savrda et al. (1984, p. 1184), this documents a strong reduction of the oxygen content of the bottom water and probably even dysaerobic conditions. After Brett & Baird (1986, fig. 11 and p. 217), a minimally aerobic to dysaerobic environment must be concluded. The oxygen content of the bottom water then must have been of the order of 1ml O_2/l or less, following the classification by Ekdale & Mason (1988, p. 720). During the sedimentation of the Sornetan Member, the water depth diminished and the bottom water became consequently more oxygenated. A normal oxygen level was probably restored when deposition of the Liesberg Member began, because this member contains a profusion of hermatypic corals. Normal marine conditions persisted thereafter in very shallow water.

2. Canton Aargau (Fig. 2)

Ammonite abundance: The first peak in ammonite abundance in Canton Aargau refers to the Schellenbrücke Bed in the excavation RG 208 of Üken AG near Herznach AG. This bed is condensed (Gygi & Marchand 1982, fig. 6) and discontinuous. It occurs neither at Auenstein AG (section RG 226 in Gygi 1973, fig. 3) nor at Holderbank AG (section RG 276 in Gygi et al. 1979, fig. 3, and in Mangold & Gygi 1997, fig. 2). This peak is then a local feature. Ammonites became again relatively abundant in the upper part of the normal facies of the Birmenstorf Member. Their frequency was established in the excavation RG 230 north of the Eisengraben near Gansingen AG (Gygi 1977, pl. 11, section 3). The figure of 5.5 ammonites per m^3 thus obtained is certainly too low, because this excavation has been made with a mechanical shovel. By this method, only larger ammonites down to the size of *Glochiceras* could be found. Smaller forms that are abundant elsewhere in the upper Birmenstorf Member were not seen. Tiny ammonites can only be found in weathered outcrops. Very few ammonites preserved as minute casts of iron sulfide (oppeliids) were found in the lower Effingen Member below the Gerstenhübelkalk Beds by J. Ogg in the road cut of section RG 226 between the quarries of Jakobsberg and Unteregg near Auenstein AG. Some ammonites occur in the Crenularis Member, but their frequency is much less than 1 ammonite per m^3. Another small maximum in ammonite abundance occurs in the marly, glauconitic limestone of the lower Baden Member. The ammonites from the large quarry of Mellikon AG were counted. The majority of these were excavated with a bulldozer. This lead to a bias in the collection towards large perisphinctids. The frequency of 1.4 ammonites per m^3 in Fig. 2 is then a minimum.

Sedimentation rate: No or only very little iron oolitic sediment was laid down in Canton Aargau during the early Oxfordian until the end of the Cordatum Subchron. Where sedimentation occurred, it was lens-like as the Schellenbrücke Bed. Widespread sedimentation at a minimal rate commenced at the beginning of the Densiplicatum Subchron of the Transversarium Chron and continued at a very low rate until the end of the Antecedens Suchron. This is when the thin (less than 10cm thick), condensed bed at the base of the Birmenstorf Member was formed. This is a regional marker bed that locally contains limonitic or chamositic iron ooids near Üken AG (section RG 208), Auenstein (section RG 226) and Holderbank AG (section RG 276). Ammonites are rare in this marker bed. Normal sedimentation at a low rate began with the Luciaeformis Subchron when the uncondensed facies of the Birmenstorf Member was laid down. The rate of sedimentation increased first gradually, then rapidly when the Effingen Member was deposited. It exceeded 2.5m per 10'000a when the middle and the upper Effingen Member was sedimented, but it is then difficult to quantify (out of scale in Fig. 2). Mud turbidites accounted for much of the sediment input during deposition of the lower (see Gygi et al. 1998, fig. 10) and middle Effingen Member. Storm layers (tempestites) are common in the upper part of the member (Gygi 1986, fig. 7). The sedimentation rate dropped dramatically after the rapid deposition of the Geissberg Member. This lead to the formation of the thin, glauconitic Crenularis Member which is a regional marker bed. Normal sedimentation of lime mud prevailed when the Wangen Member was formed. Then there occurred another abrupt fall of the sedimentation rate at the time when the interregional glauconitic marker bed of the Knollen Bed was formed. This event can be documented in northern Switzerland from east of Olten (Schönenwerd SO, section RG 28, bed 14, unpublished) to Canton Schaffhausen and from there to near Balingen in southern Germany (Gygi 1969, p. 57 and pl. 19). It is probable that the Knollen Bed is coeval with the *bauhini* faunal horizon of Schweigert & Callomon (1997, figs. 3 and 4) in southern Germany. The Kimmeridgian would then begin at the base of the Knollen Bed in northern Switzerland (Fig. 2). After the deposition of the Letzi Member at a normal rate, the sedimentation rate became again very low during deposition of the glauconitic lower Baden Member. *Sutneria platynota* (REINECKE) rarely occurs at the base of the lower Baden Member in the large quarry near Mellikon AG (section RG 70, bed 120, pl. 17 in Gygi 1969). The bulk of the lower Baden Member is formed by bed 124 of that section which contains ammonites mostly from the Hypselocyclum Zone. The sedimentation rate must then have slightly augmented sometime in the Hypselocyclum Chron.

Water depth: Gygi (1981, p. 245) concluded a depth interval of 80–100 m for the deposition of the Schellenbrücke Bed near Herznach following different, independent lines of evidence. An increasing water depth is assumed for the Early Oxfordian before the Schellenbrücke Bed was laid down, because some eustatic sea level rise and endogenic subsidence (Gygi 1986), but almost no sedimentation occurred at that time. The water depth must have increased beyond 100 m when the condensed bed at the base of the Birmenstorf Member was formed during the Densiplicatum and the Antecedens Subchrons, because a substantial eustatic sea level rise took place during the Antecedens Subchron (Gygi 1986, fig. 4) at a time when almost no sediment was laid down (Fig. 2). The condensed bed at the base of the Birmenstorf Member contains both chamositic iron ooids and glauconite. Gygi (1981, p. 243) concluded that chamosite was formed at that time in northern Switzerland down to a depth of about 100 m, and glauconite at greater depth when the sedimentation rate was low. Following the method of Gygi (1986), the depth of deposition of the normal facies of the Birmenstorf Member during the Luciaeformis Subchron can be calculated at 120 m. The heavy sedimentation rate at the deposition time of the middle and upper Effingen Member as well as the Geissberg Member caused the water depth to diminish greatly. At the end of sedimentation of the Geissberg Member the water depth must have been of the order of 10 m or less, because the uppermost Geissberg Member is a biocalcarenite in the Bözberg area (Gygi 1969, pl. 5, fig. 22). A major eustatic sea level rise during the Bimammatum Subchron caused the water depth to increase again (cf.

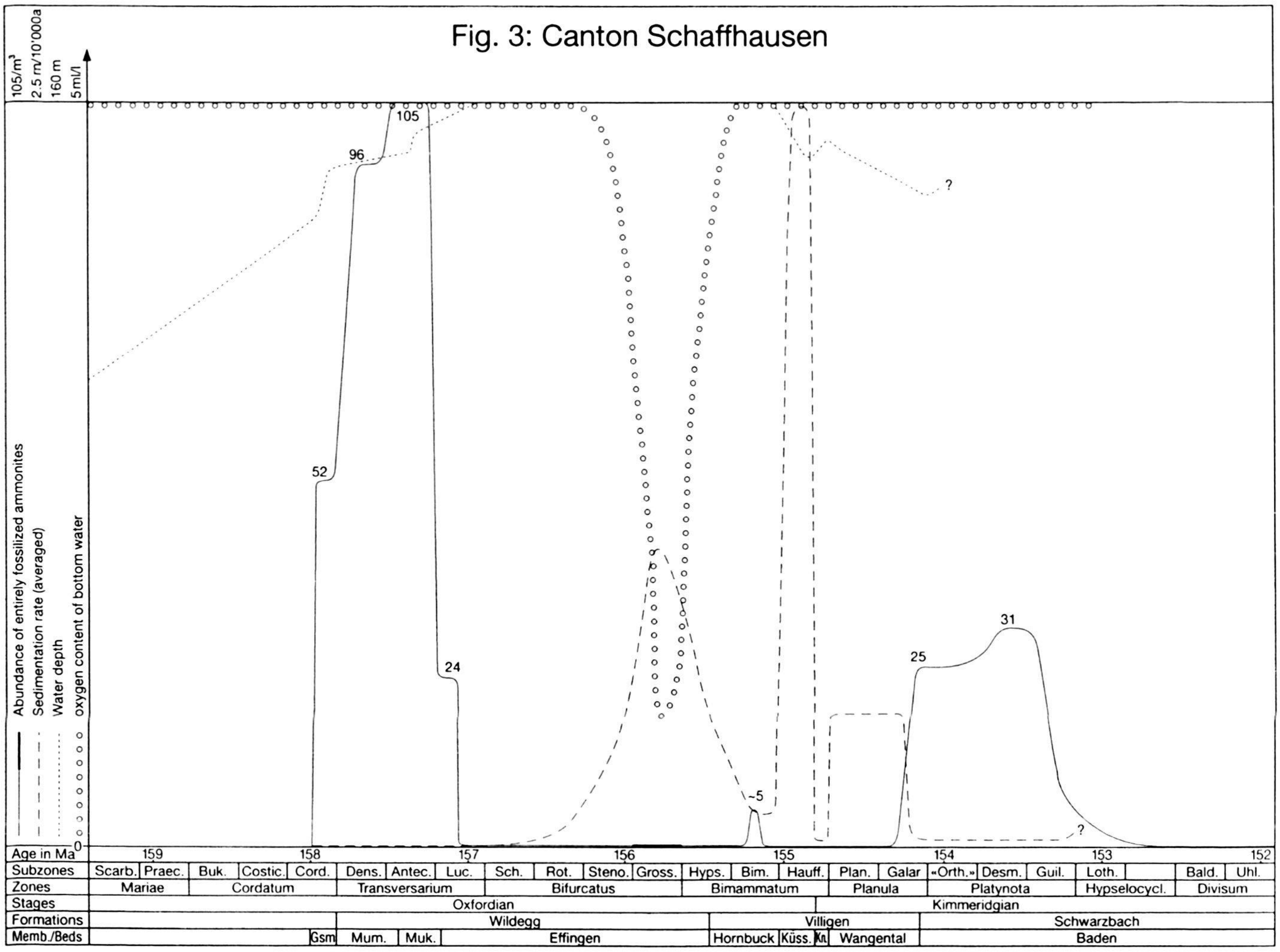

Fig. 3. Variables of sedimentation in Canton Schaffhausen.

Gygi 1986, fig. 4) to at least 30 m (Gygi 1986, p. 479). A further relative sea level rise occurred when the Letzi Member was deposited at a normal rate. The water depth at the end of deposition of the Letzi Member near Auenstein AG can be calculated to have been at least 60 m. After this time, the water depth probably further increased, because there was almost no sedimentation in this area until the Hypselocyclum Chron.

Oxygen content: The bottom water was well-oxygenated when the Schellenbrücke Bed was laid down (Gygi 1981, p. 248). The rich benthic macrofauna (dominated by siliceous sponges) of the normal facies of the Birmenstorf Member is evidence that conditions of deposition did not change noticeably in the Luciaeformis Subchron. The oxygen content of the bottom water only dropped when the sedimentation rate of the marly Effingen Member became very high. This implied a high rate of siliciclastic mud supply from land. The water depth at the beginning of sedimentation of the Effingen Member was more than 120 m (Fig. 2). The bottom of the epicontinental basin was therefore well below normal wave base, and the water above the sediment surface must normally have been quiet. Gygi (1969, p. 107) presented evidence that the bottom water of the middle Effingen Member (section RG 37, bed 54, pl. 17 in Gygi 1969) was temporarily anaerobic. Such conditions could develop in an open marine environment only if the bottom water was normally quasi-stagnant. Turbidity currents (Gygi 1969, p. 107), submarine debris flows (Gygi & Persoz 1986, figs. 2–3) and storms (Gygi 1986, fig. 7) only episodically disturbed this quiet environment. A low mean oxygen content of the bottom water of the Effingen Member is indicated by the stunted ostracods found by Oertli (1959), the rarity of benthic foraminifera (Gygi & Stumm 1965) and evidence from dinoflagellates (Ghasemi in Ghasemi et al. 1999). A considerable amount of organic matter must have been brought into the basin with the siliciclastic mud from land in the northwest. Decomposition of this organic matter consumed much of the oxygen in the bottom water. But the oxygen minimum (Fig. 2) as documented by the formation of iron sulfide ammonite steinkerns (see above) did not coincide with the maximum of the sedimentation rate of the Effingen Member that was probably reached only towards the end of deposition of the member. By the high sedimentation rate the sediment surface was raised from the dysaerobic into the aerobic zone after a certain time. Evidence for this is the appearance of benthic bivalves like *Pholodomya* and ostreids in the uppermost Effingen Member (Gygi 1969, p. 91).

3. Canton Schaffhausen (Fig. 3)

Ammonite abundance: Since the sedimentation rate was zero during most of the Early Oxfordian in Canton Schaffhausen, no ammonites could be fossilized until the Cordatum Subchron. At that time, sedimentation of the Glaukonitsandmergel Bed began at a very low rate. Ammonites are relatively abundant in this bed. Their abundance increases in the condensed Mumienmergel Bed above and reaches a maximum of 105 ammonites per m^3 in the condensed Mumienkalk Bed (Muk. in Fig. 3). This is the greatest abundance found anywhere in the Late Jurassic of northern Switzerland. Some ammonites can also be found in the glauconitic marl (10cm thick) at the base of the Effingen Member. The combined mean thickness of the Glaukonitsandmergel Bed (Gsm.), the Mumienmergel Bed (Mum.), the Mumienkalk Bed (Muk.) and the glauconitic marl at the base of the Effingen Member is only about half a meter (Gygi 1999b, fig. 2). Ammonites are again relatively common in the upper Hornbuck Member where small sponge bioherms occur. Ammonites can be found in sufficient numbers to justify an excavation in the lower Schwarzbach Formation where their numbers have been counted in the excavation RG 239 at Summerhalde near Schaffhausen.

Sedimentation rate: As stated above, there was no sedimentation at all in Canton Schaffhausen from the beginning of the Oxfordian to the Cordatum Subchron. In that subchron, sedimentation resumed, but the average rate remained very low until the end of the Luciaeformis Subchron. A relatively high sedimentation rate occurred when the marly Effingen Member was laid down, but this rate was by far surpassed at the time that the carbonate mud of the Küssaburg Member was deposited. The rate was low during the Platynota Chron, then rose to a value that cannot be calculated for lack of data in the middle and upper Schwarzbach Formation.

Water depth: At the beginning of the Oxfordian the water depth was about 100 m in Canton Schaffhausen, because the marly lenses of the Lamberti Subchron below the Glaukonitsandmergel Bed contain limonitic iron ooids and some glauconite. Gygi (1981, p. 244) concluded that about 100 m are the bathymetric limit above which iron ooids were formed and glauconite below when the sedimentation rate was low. Endogenic subsidence and eustatic rise of sea level then caused the water depth to increase, because there was no sedimentation. The depth surpassed 160 m at the end of the Transversarium Chron because of continuing relative sea level rise and minimal sedimentation (out of scale in Fig. 3). The water depth at the end of the Planula Chron has been recalculated to be 140 m (as compared with 120 m in Gygi 1986, p. 472).

Oxygen content: The fossilized macrofaunas (where they occur) are evidence that the bottom water was normally aerated except when the input of siliciclastic mud into the basin was high at the time when the bulk of the marly Effingen Member was laid down. Some ammonites were fossilized as casts of iron sulfide at that time indicating dysaerobic bottom water, but no distinct figure of oxygen content can be concluded.

Conclusions

It is apparent from Fig. 1 that the ammonites considered in this study were fossilized in greater numbers only in sediments laid down at a depth of more than about 50 m (cf. Gygi 1986, fig. 6A) where the water was cooler and changed little in temperature. Ammonite fossils are rare or even absent in sediments from very shallow water (Gygi 1995, p. 4). In deeper water, there is a correlation between the average sedimentation rate and ammonite fossilization: No fossils could be formed when there was no sedimentation at all. The fossilization of larger ammonites required a high episodic sedimentation rate of mud at the locus of fossilization. The probability of ammonite fossilization then increases with a rising mud sedimentation rate.

From this follows a paradox: Ammonite fossilization required a high local sedimentation rate, at least episodically. Otherwise, ammonite shells would probably have been rapidly destroyed by boring organisms (bioerosion, Gygi 1970, p. 35). But the optimum of ammonite fossilization in water deeper than about 50 m is reached at a very low average sedimentation rate (Figs. 1 and 3) of maybe as little as 10 mm/10'000a. When the average sedimentation rate increases only slightly to 160 mm/10'000a, the abundance of fossilized ammonites decreases markedly (Fig. 2, normal facies of the Birmenstorf Member, Luciaeformis Subchron). When it is assumed that living conditions for ammonites were good and about equal in the Schellenbrücke Bed (Sch. in Fig. 2) and in the normal facies of the Birmenstorf Member, and that the probability of ammonite fossilization was greater in the normal facies of the Birmenstorf Member because of the greater sedimentation rate, this means that the concentration not only of ammonite fossils, but also of living ammonites, was diluted if the average sedimentation rate increased to more than about 10 mm/10'000a. The main conclusions of this study are:

1) The optimal habitat of ammonites was in deeper water where the average rate of sedimentation was very low. This

corroborates the conclusion of B. Ziegler (1963, p. 102) that ammonites lived in close relation to conditions at the bottom of the sea.

2) Ammonites were primarily abundant where the sedimentation rate was about 10 mm/10'000a or less.
3) The tolerance of ammonites or, more probably, of the organisms that were their food, of high average sedimentation rates in their habitat was much less than that of some hermatypic corals (mainly platy microsolenids as in the Liesberg Member L. as documented in Fig. 1).
4) A mechanism providing for the locally and episodically high rate of sediment supply which was necessary for ammonite fossilization in deeper water with a normally very low average rate of sedimentation cannot be proposed. Particularly strong tropical storms are one possibility to explain that (Gygi 1981, p. 242).
5) The ammonites fossilized in the Renggeri Member as casts of iron sulfide were very probably living in that habitat with an oxygen content in the bottom water of the order of 1ml/l or less (Fig. 1). This means that ammonites apparently could tolerate a reduction of the oxygen content of the water in their habitat to 20% or less of the normal content. As B. Ziegler (1963, p. 98) stated, the ammonites reacted by reducing their adult size.
6) A low oxygen content in the bottom water of the basin only developed when the supply of siliciclastic mud exceeded a certain threshold as in the Renggeri and Effingen Members. A high rate of carbonate mud influx like in the Küssaburg Member (Küss. in Fig. 3) caused no noticeable reduction of the oxygen content in the bottom water.

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