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Bivalves from the Nusplingen Lithographic Limestone (Upper Jurassic, Southern Germany)

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Abstract

The bivalve fauna from the Upper Jurassic Nusplingen Lithographic Limestone (SW Swabia) is recorded for the first time. Eighteen bivalve taxa were identified, partly in open nomenclature because of their poor preservation. Besides the very common small oyster *Liostrea socialis*, randomly scattered throughout the whole section, most taxa are represented only by single or a few isolated specimens. They originated from environments in the neighbourhood of the laminated limestone deposit. Accumulations of oysters sometimes previously interpreted as "benthic islands" in analogy to similar finds from the Lower Jurassic Posidonia Shale mostly represent colonies grown on drifting empty ammonite shells. Accumulations of partly incomplete oysters together with several ammonites and/or belemnite guards also occur. They represent regurgitates of predators (probably most of them of vertebrates), which caught drifting shells and other pseudoplanktic or nektonic prey. In-situ growth of small nuculid bivalves on the sea floor is restricted to two succeeding monospecific layers. They result from a single immigration event with subsequent rapid reproduction, typical of an r-strategist.

Keywords: Bivalves, diversity, restricted environment, autecology, lithographic limestones, Jurassic.

Zusammenfassung

Aus dem oberjurassischen Nusplinger Plattenkalk der südwestlichen Schwäbischen Alb werden erstmals die Muscheln dokumentiert, die mit insgesamt bislang 18 Taxa, z. T. erhaltungsbedingt in offener Nomenklatur, belegt werden können. Neben häufigen kleinen Austern (*Liostrea socialis*), die im gesamten Profil vorkommen, sind die meisten Taxa nur durch wenige oder einzelne Individuen nachgewiesen, die aus benachbarten Faziesräumen in den Plattenkalk-Biotop hineingeraten sind. Bei den früher in Analogie zum Posidonienschiefer als „benthic islands" interpretierten Austernanhäufungen handelt es sich meistens um den Bewuchs leerer, driftender Ammonitenschalen. Manchmal finden sich auch Anhäufungen von teilweise zerbrochenen Austern zusammen mit mehreren Ammoniten und/oder Belemnitenrostren, die als Speiballen (meistens wohl von Wirbeltieren) angesprochen werden können. Ein autochthones Vorkommen von kleinen nuculiden Muscheln am Meeresboden der Plattenkalk-Wanne ist hingegen auf zwei unmittelbar aufeinanderfolgende Lagen beschränkt, die auf ein einziges Einwanderungsereignis zurückgeführt werden. Dieses kurzzeitige Einwandern mit massenhafter Vermehrung ist typisch für einen r-Strategen.

Contents

1. Introduction

The Nusplingen Lithographic Limestone, situated in the south-western part of the Swabian Alb (Fig. 1; Geological Maps of Baden-Wuerttemberg no. 7819 Messstetten, SCHWEIZER 1994) represents the only deposit of fossil-bearing lithographic limestones in the Swabian Jurassic. Systematic scientific excavations by the National History Museum of Stuttgart (SMNS) are carried out since 1993 at two localities of this fossillagerstätte (two quarries near the villages of Nusplingen and Egesheim) (DIETL et al. 1998). One of the aims of these excavations is to document

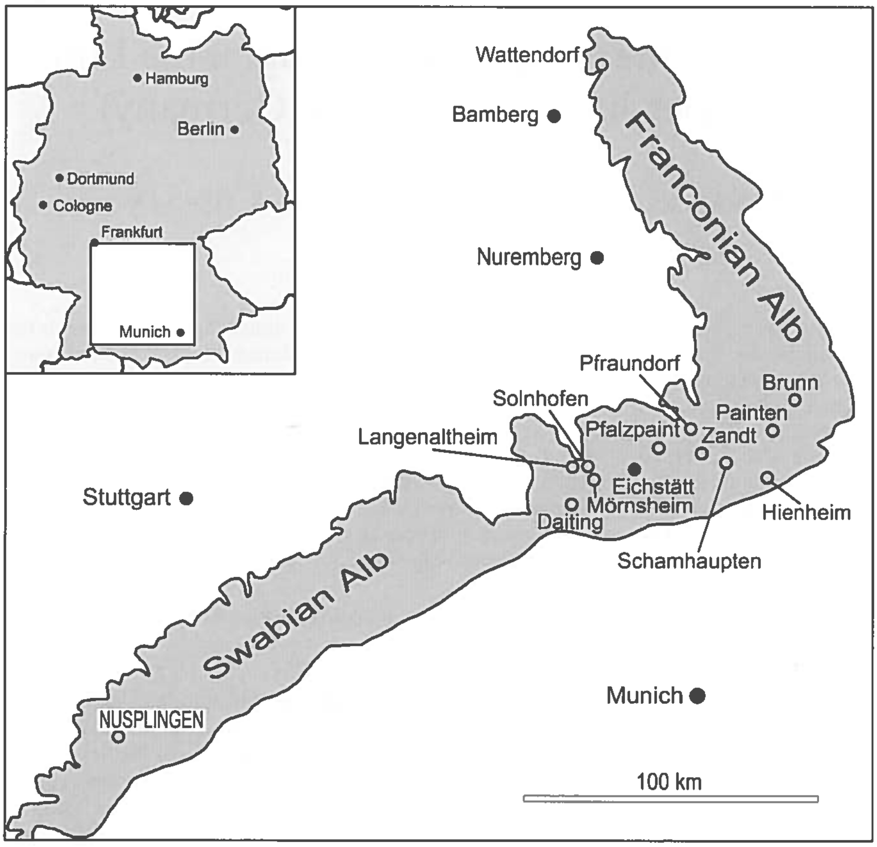

Fig. 1. Location of the Nusplingen site and further Plattenkalk localities in the Upper Jurassic of southern Germany (modified from FÜRSICH et al. 2007b).

the whole fossil inventory, its distribution, and possible changes through the whole section (for section see Fig. 2). A description of the current state of knowledge about these lithographic limestones can be found in DIETL & SCHWEIGERT (1999, 2001, 2004). In DIETL & SCHWEIGERT (2001), all taxa identified until spring 2001 are listed. By 2008, however, the number of recorded taxa has reached ca. 350.

During earlier excavations in the Nusplingen Lithographic Limestone, the focus was not on inconspicuous invertebrate groups such as the bivalves. This created a distorted picture of the faunal composition. Until now, a description of the bivalve fauna is missing. Among the old collections, there were nearly no bivalves. Therefore, this overview is based almost exclusively on new finds from recent excavations.

Compared to other finds from the Nusplingen Lithographic Limestone such as nektonic molluscs (ammonites and their aptychi and belemnites), drifted exuviae of penaeid shrimps (*Antrimpos undenarius*), and different types of coprolites, the mainly benthic bivalves are less common. Only accumulations of *Liostrea socialis* (so-called "shell nests"), also known from other Late Jurassic lithographic limestone deposits, were noticed in the past. Both FRAAS (1855) and QUENSTEDT (1857) recorded hardly any other bivalves. Also WALTHER (1904) only mentioned the oysters. Finally, in the otherwise comprehensive fossils list of ENGEL (1908), bivalves are missing completely. Only FAHRION (1937) and KAUFFMAN (1978) have worked on the oyster accumulations. FAHRION interpreted them as a sign of living oysters, which were attracted by carrion on the seafloor and then became themselves victims of the hostile conditions. However, this theory is incompatible with the physiology of oysters. KAUFFMAN discussed his "benthic-island-model", which he had developed for the Early Jurassic Posidonia Shale. According to this model the bivalves were living on secondary hardgrounds on the sediment surface, and thus were autochthonous. In the case of his specimen from the Nusplingen Lithographic Limestone, KAUFFMAN did not exclude that these accumulations might also be the remains of meals of predators.

In this study, we try to find a plausible interpretation for the origin of these oyster accumulations. Therefore, a representative sample out of the abundant fossil material was selected. As it is very time consuming to prepare this material, which is usually covered by sediment (Fig. 3),

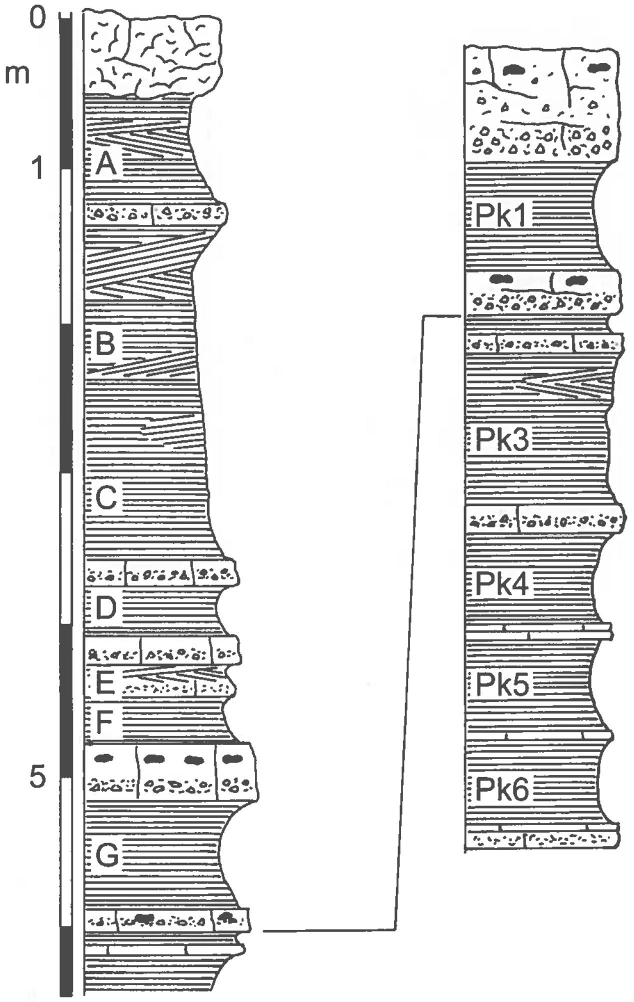

Fig. 2. Sections and correlation of the Nusplingen Lithographic Limestone in the Nusplingen quarry (left) and Egesheim quarry (right). Bed numbers of the laminated limestones after ALDINGER (1930) and DIETL et al. (1998), turbidite breccia beds (black: flint nodules) or bioturbated limestones separating the laminated limestones unnumbered.

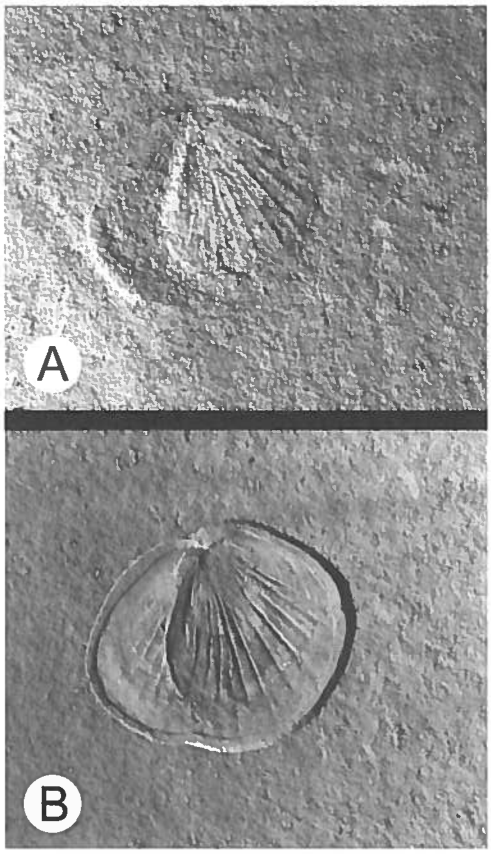

Fig. 3. Preservation of bivalves in the Nusplingen Lithographic Limestone. Usually, the fossils are covered with sediment which has to be removed mechanically. *Ctenostreon pectiniforme* (SCHLOTHEIM), juvenile specimen; Nusplingen quarry; Bed G, 70–78 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64549. – **A**. Before preparation. **B**. After preparation. – × 1.

and many specimens are even undetectable, a statistical treatment was not possible.

Bivalves from Franconian laminated limestone deposits ("Solnhofen-type limestones") have been documented by FRICKHINGER (1994, 1999), RÖPER et al. (1996, 1999), and RÖPER & ROTHGAENGER (1998), but they remained unassigned. They also show only little resemblance to the taxa from the Nusplingen Lithographic Limestone (see below). Most recently, FÜRSICH et al. (2007a, b) and VIOHL & ZAPP (2006, 2007) provided compilations of the faunas from the Kimmeridgian plattenkalks of Wattendorf in northern Franconia and those of Schamhaupten, east of Eichstätt, respectively. New systematic and specific palaeoecological works on Late Jurassic bivalve faunas from SW Germany exist only for a few localities (Biburg, Laisacker, Neuburg/Donau, e. g. FISCHER 1998; HURST 1992; HÖLDER 1990; JOHNSON 1984; WELLNHOFER 1964; YAMANI 1975, 1982, 1983). Therefore, a comparison of taxa occurring in the Nusplingen Lithographic Limestone with material from other occurrences of Jurassic sediments from SW-Germany primarily deals with unpublished data from collections and own field observations.

Abbreviations

IFGT Institut für Geowissenschaften der Universität Tübingen, Germany.

SMNS Staatliches Museum für Naturkunde Stuttgart, Germany.

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Ms. R. Harling (SMNS) for taking some of the photographs. We are greatly indebted to Dr. A. Liebau (Tübingen) who lent us comparative material and provided access to material from earlier excavations in the Nusplingen Lithographic Limestone. We also thank Ms. J. Howes for checking the English language. We are very grateful to the useful improvements suggested by the two referees, Prof. Dr. F. T. Fürsich (Erlangen) and Dr. G. Delvene (Madrid) and the journal's editor, Dr. R. Böttcher (Stuttgart). The excavation of the Natural History Museum of Stuttgart and the study of the finds have been generously supported by the Deutsche Forschungsgemeinschaft (project Di 680/1).

2. Systematic palaeontology

Family Nuculidae Gray, 1824

Nuculidae gen. et sp. indet.
Fig. 4

v 2001 Nuculidae gen. et sp. indet. – Dietl & Schweigert, p. 70. – [Nusplingen]

Material: Numerous large slabs with numerous specimens from Bed L of the Nusplingen quarry.

The specimens have a rounded triangular outline and show no details of the hinge. Because of its poor preservation and small size of at most 7 mm in length, a more precise assignment is not possible. Some better preserved specimens show a slightly curved umbo. A comparison with material from the "Zementmergel Formation" showed that these bivalves probably represent nuculid bivalves.

The extensive occurrence of this small taxon is very surprising. Up to 500 specimens per square meter can be found on one bedding plane. Some of the commonly articulated bivalves are still with both valves closed, whereas others are gaping. In contrast to all other bivalves from Nusplingen in double-valve preservation, these nuculids are predominantly embedded in convex-up position. In very few cases, an indistinct crawling lane with a length of a few centimetres can be seen behind the moulds. There are no similar traces found in other strata of the Nusplingen Lithographic Limestone. A few poorly preserved articulated specimens of the same species appear on a bedding plane 5 mm above the first layer. The moulds all have the same outline, but are conspicuously larger than the ones of the lower layer. They may represent survivors of the older population. This interpretation requires a high sedimentation rate, which has been proven by biostratinomic analyses of vertically embedded belemnite rostra (cf. Schweigert 1999b). The bioturbation caused by the bivalves disturbed the lamination of the limestone only for a very short time.

The mass occurrence of this nuculid species resembles that of r-strategists, although nuculids are not expected to represent r-strategists. Similar examples from the Nusplingen laminated limestone are the so far endemic echinoid *Polycidaris nusplingensis* (cf. Schweigert 1998; Grawe-Baumeister et al. 2000), and the producers of some ichnotaxa (e. g., *Parahaentzschelinia egesheimense*, see Schweigert 1998).

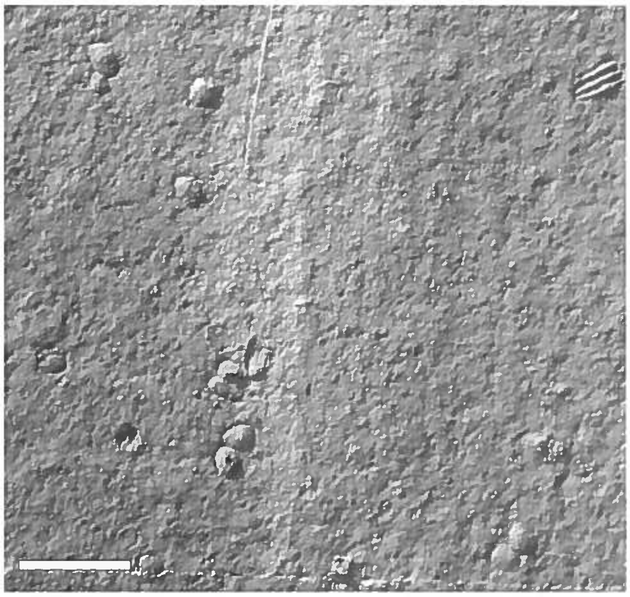

Fig. 4. Mass occurrence of a small nuculid (Nuculidae gen. et sp. indet.) on upper surface of a layer; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed L, 5–10 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64412. – Scale: 20 mm.

Nuculana (Rollieria) sp.

Material: 1 specimen from the Nusplingen quarry, Bed G, 10–20 cm below top; comparative material from the Zementmergel Formation of Münsingen (Central Swabian Alb).

The only specimen of *Nuculana (Rollieria)* sp. is a single valve, which has a length of 8.5 mm and a height of 5 mm, and is embedded in convex-down position.

A preparation of this specimen is not possible, as it is preserved as internal mould. However, its outline excludes an allocation to the previously described nuculid taxon forming a mass-occurrence. In contrast to the latter, this single-valved specimen is an allochthonous faunal element. Comparable forms also occur in the coeval Zementmergel Formation, which may have represented the original habitat of this taxon.

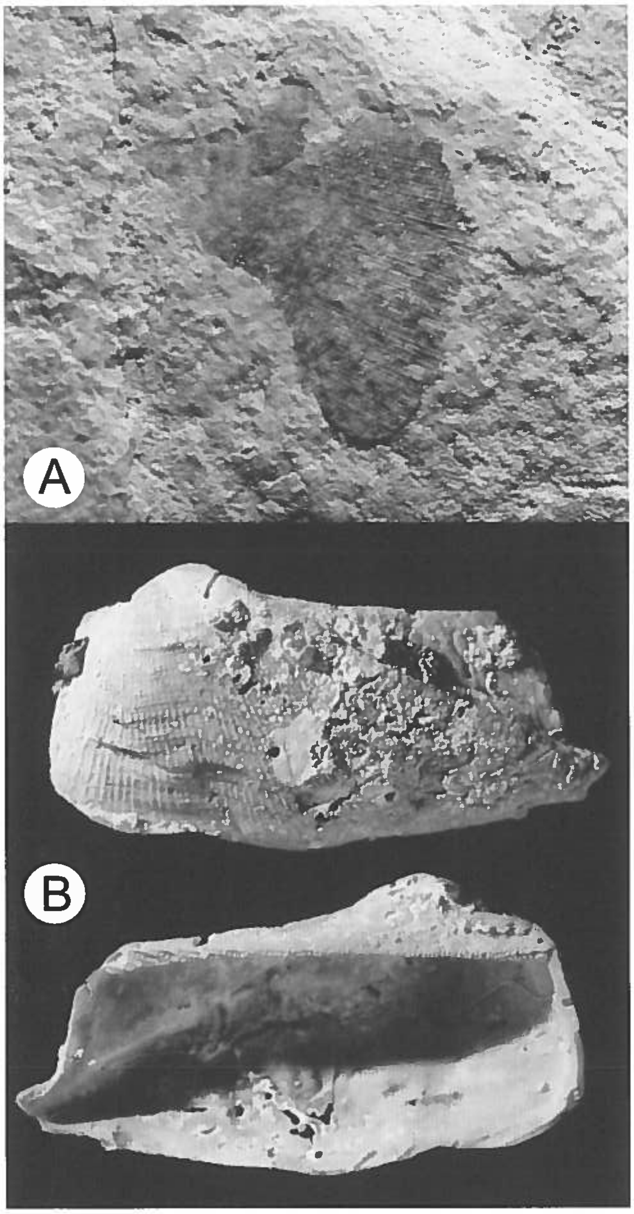

Fig. 5. *Arca (Eonavicula) fracta* (GOLDFUSS). – **A**. Cf.-specimen, a small shell fragment; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed D, 0–10 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64454. **B**. Complete specimen, outer and inner view of left valve; Nattheim; coral limestone; Upper Kimmeridgian, Ulmense Subzone; SMNS 67340 (leg. KÖSTLIN). – Fig A: × 2, Fig. B: × 1.

Family Arcidae LAMARCK, 1809
Genus *Arca* LINNÉ, 1758

Arca (Eonavicula) cf. *fracta* GOLDFUSS, 1833
Fig. 5

cf. *1833 *Arca fracta* sp. nov. – GOLDFUSS, p. 121, pl. 121, fig. 10.
cf. 1857 *Arca fracta*. – QUENSTEDT, p. 759.
cf. 1908 *Arca fracta* GOLDF. – ENGEL, p. 457.
v 2001 *Parallelodon fractus* (GOLDFUSS). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]

Material: 2 fragmentary specimens from the Nusplingen quarry, Bed D; 1 left valve as comparative material from the Upper Kimmeridgian coral limestones of Nattheim (Fig. 5B).

The two small shell fragments show a rough reticulate pattern on their exterior shell, which is characteristic of the family Arcidae. After careful comparison with complete specimens of different species of the genera *Arca (Eonavicula)*, *Barbatia*, *Nenodon*, and *Stenocolpus* (e. g. WELLNHOFER 1964; YAMANI 1982) from the Upper Jurassic of Nattheim and other localities in SW Germany they could only be tentatively assigned to the rare species *Arca (Eonavicula) fracta* GOLDFUSS. Both specimens come from the bituminous layer D that does not contain many other bivalve taxa. Because of the fragmentary preservation, we assume that the fragments most likely result from predatory activity outside the lagoon, but it cannot be excluded that the fragments were washed in during storms.

Family Pinnidae LEACH, 1819
Genus *Pinna* LINNÉ, 1758

Pinna sp.
Fig. 6

v 2001 *Pinna* sp. – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]

Material: 1 specimen from the Nusplingen quarry, Bed L; comparative material from the "Liegende Bankkalke Formation" of the western Swabian Alb.

Pinna is only represented by a small shell fragment showing a very typical radial pattern, which is diagnostic for this genus. Similar to *A. (E.) fracta* GOLDFUSS (see above), fragmentation might have been caused by a predator.

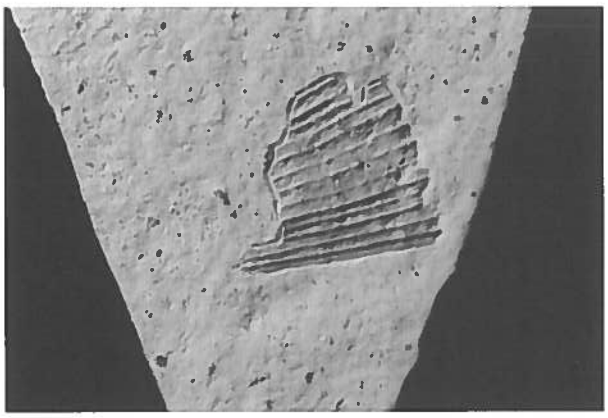

Fig. 6. *Pinna* sp., shell fragment; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed L, 40–50 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 67341. – × 2.

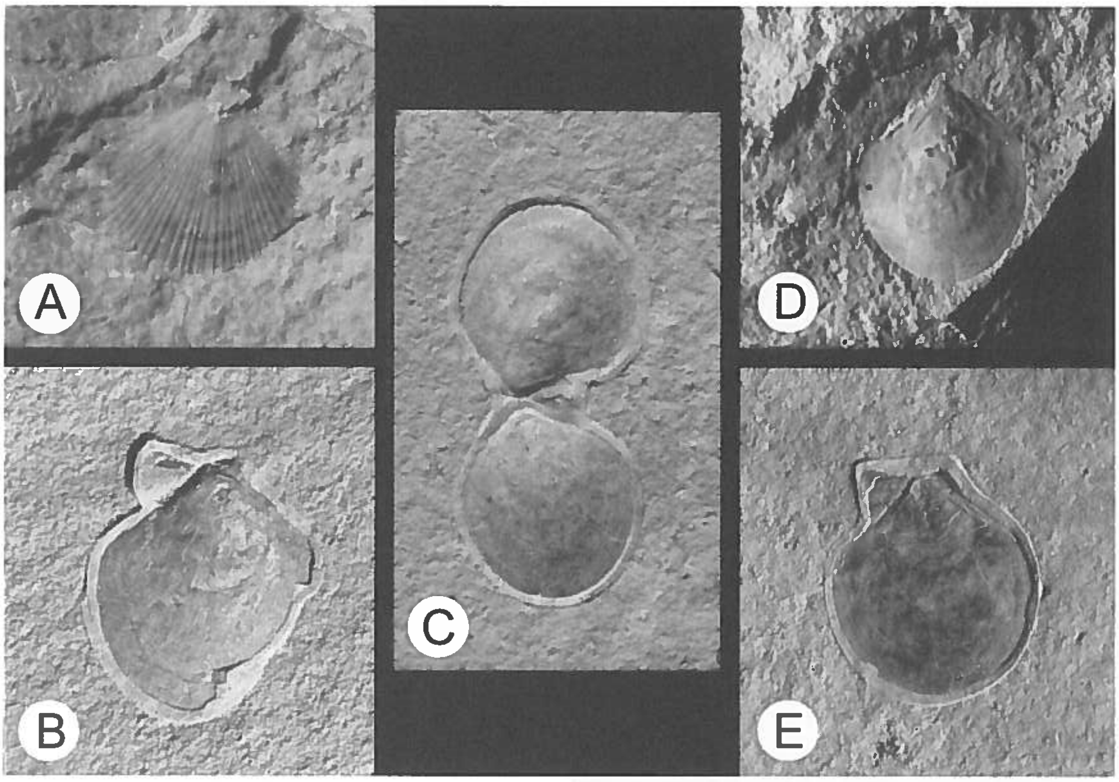

Fig. 7. Pectinids from the Nusplingen Lithographic Limestone, Upper Kimmeridgian, Ulmense Subzone. – **A.** *Chlamys textoria* (SCHLOTHEIM); Nusplingen quarry; Bed K4; SMNS 64558. **B.** *Camptonectes auritus* (SCHLOTHEIM); Nusplingen quarry; Bed G, 40–50 cm below top; SMNS 67342. **C.** *Camptonectes auritus* (SCHLOTHEIM); Egesheim quarry; Bed Pk 4, 15–20 cm below top; SMNS 67343. **D.** *Propeamussium nonarium* (QUENSTEDT); Nusplingen quarry; Bed G, 20–30 cm below top; SMNS 67344. **E.** *Cingentolium cingulatum* (GOLDFUSS); Nusplingen quarry; Bed G, 70–78 cm below top; SMNS 67252. – Figs. A–D × 2, Fig. E × 1.

In the "Bankkalk" facies of the Swabian Upper Jurassic, *Pinna* is relatively rare and generally of small size. In contrast, *Pinna quadrata* SCHNEID, 1915 is very common in the micritic bedded limestones of the Lower Tithonian Rennertshofen and Neuburg formations in southern Franconia, and is often preserved in life position.

Family Propeamussiidae TUCKER ABBOTT, 1954
Genus *Propeamussium* DE GREGORIO, 1884

Propeamussium nonarium (QUENSTEDT, 1857)
Fig. 7D

*1857 *Pecten nonarius*. – QUENSTEDT, p. 795, pl. 98, fig. 4.
1964 *Variamussium nonarium* (QUENSTEDT) 1858. – WELLNHOFER, p. 37, pl. 2, figs. 4–7; text-fig. 21.
1984 *Propeamussium nonarium* (QUENSTEDT, 1858). – JOHNSON, p. 32, pl. 1, figs. 13–14.
2006 *Propeamussium (Propeamussium) nonarium* (QUENSTEDT, 1858). – VIOHL & ZAPP, p. 73.
v 2007 *Propeamussium nonarium* (QUENSTEDT, 1858). – VIOHL & ZAPP, p. 135.

Material: 1 specimen from the Nusplingen quarry, Bed G. Comparative material from the Neuburg Formation (Uppermost Lower Tithonian), Unterhausen near Neuburg an der Donau (Bavaria).

The only specimen of this species from Nusplingen is the internal mould of a presumably left valve, which shows the typical widely spaced internal ribs. The shell had been dissolved during diagenesis, and the hinge region has been slightly squeezed and disrupted. In the concave interior, there are small bioclasts, which were brought in together with the small shell. This species is extremely rare in the whole Swabian Jurassic. In contrast, there are about 100 specimens known from the Franconian Neuburg Formation alone (WELLNHOFER 1964).

The holotype of *P. nonarium*, which is unfortunately missing, was found in the Zementmergel Formation at Ulm-Söflingen, which is of the same age as the Nusplingen Lithographic Limestone.

Family Pectinidae WILKES, 1810
Genus *Chlamys* ROEDING, 1798

Chlamys textoria (SCHLOTHEIM, 1820)
Fig. 7A

*1820 *Pectinites textorius* sp. nov. – SCHLOTHEIM, p. 229.
1991 *Chlamys textoria* (SCHLOTHEIM). – LAUXMANN, p. 165.
1995 *Chlamys (Chlamys) textoria* (SCHLOTHEIM 1820). – JAITLY et al., p. 197, pl. 20, figs. 3–7. – [See for synonymy list]
v 2001 *Chlamys textoria* (SCHLOTHEIM). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]
2001 *Chlamys (Chlamys) textoria* (SCHLOTHEIM 1820). – DELVENE, p. 70, pl. 4, figs. 4, 8.
v 2006 *Chlamys (Chlamys) textoria* (SCHLOTHEIM 1820). – VIOHL & ZAPP, p. 73.
2007 *Chlamys (Chlamys) textoria* (SCHLOTHEIM, 1820). – HEINZE, p. 78, text-fig. 2G.

Material: 1 specimen from the Nusplingen quarry, Bed K 4; extensive comparative material from the Upper Jurassic of different localities of the Swabian and Franconian Alb.

The only representative of this species is a single valve that had been embedded in a coarse breccia layer. The umbo and both auricles are missing. Probably, they were broken off during the transport. Therefore, this bivalve is probably allochthonous. In contrast to comparative material from the Upper Jurassic, this specimen has a conspicuously greater length-height ratio.

Genus *Camptonectes* AGASSIZ in MEEK, 1864

Camptonectes (Camptonectes) auritus (SCHLOTHEIM, 1813)
Fig. 7B, C

*1813 *Chamites auritus* sp. nov. – SCHLOTHEIM, p. 103.
v 1983 *Camptonectes auritus* (SCHLOTHEIM). – YAMANI, p. 17, pl. 2, figs. 1–4.
1984 *Camptonectes (Camptonectes) auritus* (SCHLOTHEIM 1813). – JOHNSON, p. 113, pl. 3, figs. 25–40. – [See for extensive synonymy list]
1995 *Camptonectes auritus* (SCHLOTHEIM). – JAITLY et al., p. 194, pl. 19, figs. 1–4.
v 2001 *Camptonectes auritus* (SCHLOTHEIM). – DIETL & SCHWEIGERT, p. 70, text-fig. 69. – [Nusplingen]
? 2001 *Camptonectes (Camptonectes) auritus* (SCHLOTHEIM 1813). – DELVENE, p. 69, pl. 4, fig. 5.
2007 *Camptonectes (Camptonectes) auritus* (SCHLOTHEIM, 1813). – HEINZE, p. 76, fig. 2A–E.

Material: 1 specimen from the Nusplingen quarry, Bed G, 1 specimen from the Egesheim quarry, Bed Pk 4; comparative material from the microbial-sponge limestones of Biburg (Bavaria).

Camptonectes (Camptonectes) auritus does not wear any other ornamentation except concentric growth lines on the interior of the shell, whereas the outer surface exhibit characteristic divaricate striae. The right valve shows the typical anterior auricle (YAMANI 1983). Because of the deep byssal notch, this species had probably been attached to a hard substrate by its byssus.

At least the specimen from the Nusplingen quarry was possibly brought in by a predator, as the anterior margin is broken off. This injury obviously took place in the water column before the embedding, and not at the place of final burial.

C. (C.) auritus is a regionally widespread species, and had been described by YAMANI (1983) from the Oxfordian and the Lower Kimmeridgian of Bavaria. As the specimens from the Nusplingen Lithographic Limestone are of Late Kimmeridgian age, they are the youngest representatives of this species so far. In comparison to other Upper Jurassic limestones, *C. (C.) auritus* is extremely rare in the Nusplingen Lithographic Limestone.

Genus *Cingentolium* YAMANI, 1983

Cingentolium (Cingentolium) cingulatum (GOLDFUSS, 1835)
Fig. 7E

*1835 *Pecten cingulatus* PHILIPS. – GOLDFUSS, p. 74, pl. 99, fig. 3.
1983 *Cingentolium (Cingentolium) cingulatum* (GOLDFUSS) 1835. – YAMANI, p. 7, text-figs. 1–3, pl. 1, figs. 1–5. – [See for extensive synonymy list]
v 2006 *Entolium (Cingentolium)* sp. – VIOHL & ZAPP, p. 73.

Material: 1 articulated specimen from the Nusplingen quarry, Bed G, embedded in convex-down position; numerous comparative samples from the whole Upper Jurassic of the Swabian and Franconian Alb.

The articulated specimen is the only representative of this species from the Nusplingen Lithographic Limestone. It represents a very large (height: c. 30 mm) and obviously adult individual. The two valves are not gaping so that both the right valve is mostly covered by the left. The left valve shows some injuries at the margin that must have occurred before final burial.

This specimen was probably brought in by a predator, as the valves would have been separated and were not damaged by passive dropping.

Genus *Eopecten* DOUVILLÉ, 1897

Eopecten velatus (GOLDFUSS, 1833)
Figs. 8, 16

*1833 *Pecten velatus* sp. nov. – GOLDFUSS, p. 45, pl. 90, fig. 2.
v 1857 *Pecten velatus*. – QUENSTEDT, p. 801. – [Nusplingen]

Fig. 8. *Eopecten velatus* (GOLDFUSS), fragment of a very large left valve, specimen of QUENSTEDT (1857: 801); Nusplingen Lithographic Limestone; Upper Kimmeridgian, Ulmense Subzone; IFGT 1873. – Scale: 20 mm.

1975 *Eopecten subtilis* (BOEHM). – YAMANI, p. 67, pl. 4, fig. 1.
1984 *Eopecten velatus* (GOLDFUSS). – JOHNSON, p. 150, pl. 5, figs. 4–5 and 7–8. – [See for exhaustive synonymy list]
1991 *Eopecten velatus* (GOLDFUSS). – LAUXMANN, p. 165.
1992 *Eopecten velatus* (GOLDFUSS, 1833). – HURST, p. 75, pl. 2, figs. 7–12; pl. 3, figs. 1–5; pl. 4, figs. 1–5.
1994 *Eopecten subtilis* (BOEHM). – FRICKHINGER, p. 73, text-figs. 89–90.
1995 *Eopecten velatus* (GOLDFUSS 1833). – JAITLY et al., p. 196, pl. 19, figs. 5, 9–11; pl. 20, fig. 1. – [See for extensive synonymy list]
v 2001 *Eopecten velatus* (GOLDFUSS). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]
2001 *Eopecten velatus* (GOLDFUSS 1833). – DELVENE, p. 72, pl. 4, fig. 9.
v 2006 *Eopecten* sp. – VIOHL & ZAPP, p. 73.
2007 *Eopecten velatus* (GOLDFUSS, 1833). – HEINZE, p. 75, fig. 1A–E.

Material: 2 specimens from the Nusplingen quarry, Bed L and unknown bed; extensive comparative material from microbial-sponge reefs and bedded limestones of the Upper Jurassic of the Swabian Alb.

QUENSTEDT (1857) already mentioned this species from the Nusplingen Lithographic Limestone, but he had only the fragment of a right valve (Fig. 6). Apparently, it had been embedded in the laminated limestone as a fragment. Similarly to *Parallelodon* and *Camptonectes* described above, the fragment was obviously brought in by a predator. This specimen exhibits a large size pointing to favourable living conditions. In the studied comparative material from Upper Jurassic microbial-sponge reefs and adjacent limestones, *Eopecten velatus* never reaches comparable sizes. Together with *Liostrea roemeri* (QUENSTEDT), and *Nanogyra virgula* (DEFRANCE), a second specimen had been found attached to the exterior shell of a large *Aspidoceras* (Fig. 16). The bivalve was probably not byssally attached, as the two valves would have been both separated from its raft after death. Therefore, it was probably cemented directly onto the ammonite conch (cf. HARPER & PALMER 1993). *Eopecten* represents the first generation of epibionts, and was later partly overgrown by *Liostrea roemeri*.

Genus *Spondylopecten* ROEDER, 1882

Spondylopecten palinurus (D'ORBIGNY, 1850)
Fig. 9

*1850 *Pecten palinurus* sp. nov. – D'ORBIGNY, p. 342.
1984 *Spondylopecten (Spondylopecten) palinurus* (D'ORBIGNY, 1850). – JOHNSON, p. 92, pl. 3, figs. 8–14. – [See for extensive synonymy list]
1991 *Spondylopecten palinarus* (D'ORBIGNY) [sic]. – LAUXMANN, p. 165.
1995 *Spondylopecten (Spondylopecten) palinurus* (D'ORBIGNY 1850). – JAITLY et al., p. 194, pl. 18, figs. 16–18.
v 2001 *Spondylopecten palinurus* (D'ORBIGNY). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]

Material: 1 specimen from the Nusplingen quarry, Bed G; comparative material from the Upper Kimmeridgian coral limestones of Nattheim and from the Numismalismergel Formation (Lower Pliensbachian) near Göppingen (Swabia).

Spondylopecten palinurus (D'ORBIGNY) is very rare in the uppermost Jurassic of Southern Germany. The only specimen from Nusplingen is a fragmented, juvenile valve, which was probably brought to the deposition area by a predator. In comparison to *S. subspinosus* (SCHLOTHEIM), which is much more abundant in coeval strata, it shows conspicuous fine radial striae between the spinose ribs.

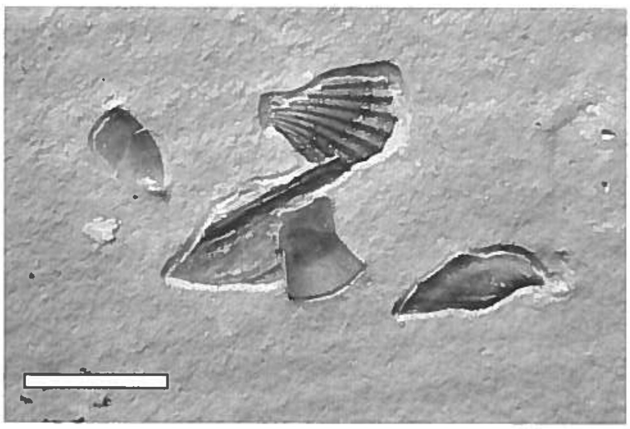

Fig. 9. *Spondylopecten palinurus* (D'ORBIGNY), fragmented specimen; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed G, 0–10 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64541. – Scale: 10 mm.

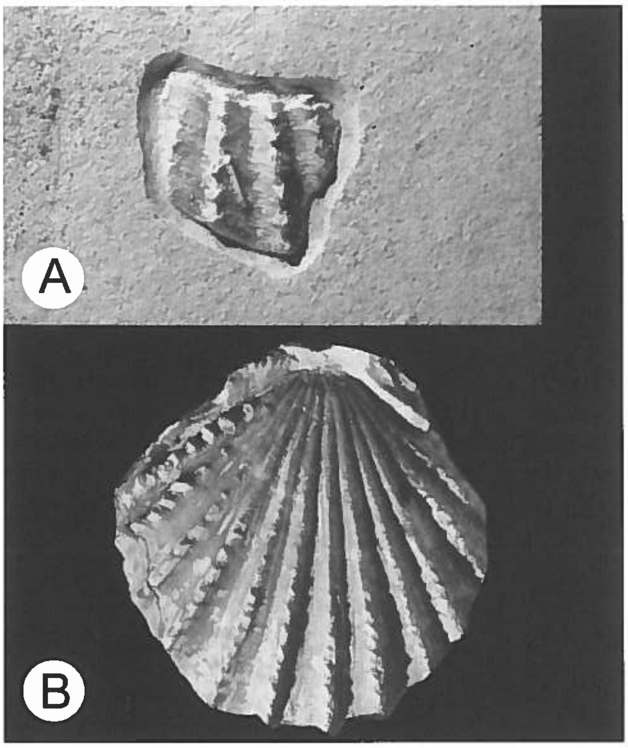

Fig. 10. *Radulopecten sigmaringensis* (ROLLIER). – **A**. Shell fragment with tiny echinoid spine; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed F, 0–5 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64427. **B**. Complete, articulated specimen; Schelklingen-Sotzenhausen; coral limestones; Upper Kimmeridgian; SMNS 21904/1. – Fig. A: × 2, Fig. B: × 1.

Genus *Radulopecten* ROLLIER, 1911

Radulopecten sigmaringensis (ROLLIER, 1915)
Fig. 10

v 1857 *Pecten subarmatus*. – QUENSTEDT, p. 754, pl. 92, figs. 8–9 [holotype].
v *1915 *Pecten (Aequipecten) Sigmaringensis* sp. nov. – ROLLIER, p. 474.
1926 *Aequipecten subarmatus* (MÜNSTER) GOLDFUSS 1834/40. – STAESCHE, p. 68.
1984 *Radulopecten sigmaringensis* (ROLLIER). – JOHNSON, p. 216, pl. 11, figs. 5–6.
v 2001 *Radulopecten sigmaringensis* (ROLLIER). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]
2001 *Radulopecten sigmaringensis* (ROLLIER 1915). – DELVENE, p. 74, pl. 4, fig. 10.

Material: 1 specimen from the Nusplingen quarry, Bed F (Fig. 10A); comparative material from the Liegende Bankkalke and Zementmergel formations near Gerhausen, the 'Nollhof Facies' from Hohrain near Sigmaringen (type locality), the Hangende Bankkalke Formation from Einsingen near Ulm, and from coral limestones of Nattheim and Schelklingen-Sotzenhausen (Fig. 10B).

The only specimen of *R. sigmaringensis* from the Nusplingen Lithographic Limestone is an isolated shell fragment. The fragment may have been brought into the basin by predators, as the surrounding strata show no bioturbation and have a very high kerogen content. A small echinoid spine is lying on the shell fragment. It might have been brought in at the same time as the shell fragment. *R. sigmaringensis* occurs in the Upper Jurassic coral facies and particularly in high energy, coarse detrital limestines, the so-called 'Nollhof Facies' (ROLL 1931).

Family Limidae RAFINESQUE, 1815
Genus *Plagiostoma* J. SOWERBY, 1814

Plagiostoma pratzi (BOEHM, 1881)
Fig. 11

*1881 *Lima pratzi* n. sp. – BOEHM, p. 179, pl. 37, fig. 6a–h.
1975 *Plagiostoma pratzi* (BOEHM, 1881). – YAMANI, p. 77, pl. 4, fig. 15; text-fig. 24. – [See for extensive synonymy]
1995 *Plagiostoma pratzi* (BOEHM). – SCHWEIGERT & SCHERZINGER, p. 316.
v 2001 *Plagiostoma pratzi* (BOEHM). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]
2001 *Plagiostoma pratzi* (BOEHM 1881). – DELVENE, p. 62, pl. 3, fig. 4.
v 2007 *Plagiostoma pratzi* (BOEHM). – DIETL et al., pl. 1, fig. 1. – [Nusplingen]

Material: 5 specimens from the Nusplingen quarry, beds E, F, L, only one of which is articulated (Fig. 11B); comparative material from the Massenkalk Formation (Upper Kimmeridgian – Lower Tithonian) and the Hangende Bankkalke Formation (Lower Tithonian) of the Swabian Alb (Fig. 11C).

All specimens of *Plagiostoma pratzi* (BOEHM) show calcitic shell preservation. In one specimen, the hinge region has been broken off facet-like. In another juvenile specimen, the ventral margin has been partly broken off. As the sediment is very fine-grained, both injuries can only be explained by an attack of a predator before burial (see above). Another single-valved specimen, however, has been found in a tempestite layer. It had probably been reworked mechanically and was then deposited in the lagoonal area.

Like other species of *Plagiostoma*, *P. pratzi* was probably epibyssate (pers. comm. F. FÜRSICH).

Genus *Pseudolimea* ARKELL in DOUGLAS & ARKELL, 1932

Pseudolimea duplicata (J. de C. SOWERBY, 1827)
Fig. 12

*1827 *Plagiostoma duplicata* sp. nov. – J. DE C. SOWERBY, p. 114, pl. 559, fig. 3.
1857 Radial gestreifte Bivalve [?*Monotis*]. – QUENSTEDT, p. 801. – [Nusplingen]

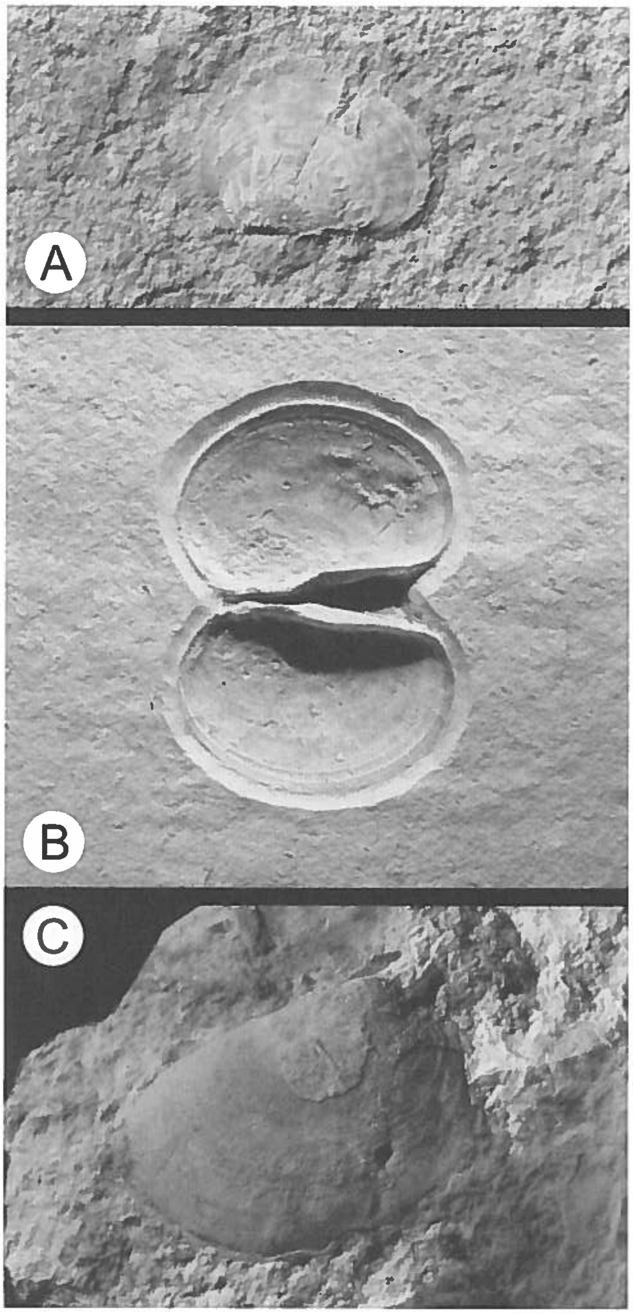

Fig. 11. *Plagiostoma pratzi* (BOEHM). – **A**. Nusplingen quarry; Nusplingen Lithographic Limestone, Bed F, 10–20 cm below top, lower surface of a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 67345. **B**. Nusplingen quarry; Nusplingen Lithographic Limestone, Bed L, 10–20 cm below top, upper surface a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 66125. **C**. Rohrdorf near Messkirch; Hangende Bankkalke Formation; Lower Tithonian, Moernsheimensis Subzone; SMNS 67346 (leg. G. SCHWEIGERT). – Fig A: × 2, Figs. B–C: × 1.

1975 *Limea duplicata* (MÜNSTER, 1835). – YAMANI, p. 76, pl. 4, fig. 13. – [See for extensive synonymy list]

1995 *Pseudolimea duplicata* (J. DE C. SOWERBY, 1827). – JAITLY et al., p. 183, pl. 13, figs. 3–5.

v 2001 *Pseudolimea duplicata* (GOLDFUSS). – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]

2001 *Pseudolimea duplicata* (J. DE C. SOWERBY 1827). – DELVENE, p. 64, pl. 3, fig. 5.

v 2006 *Pseudolimea* sp. – VIOHL & ZAPP, p. 73.

2007a *Pseudolimea* sp. – FÜRSICH et al., p. 101, 109, fig. 9B, tables 2–3.

2007b *Pseudolimea* sp. – FÜRSICH et al., p. 57, fig. 8B.

Material: More than 30 mostly articulated specimens from the Egesheim and Nusplingen quarries, and from the outcrop 'Großer Kirchbühl', all embedded in convex-down position; comparative material from the Obere Felsenkalke Formation (Upper Kimmeridgian) of Herrlingen-Lautern near Ulm (Fig. 12D).

Besides *Liostrea*, the limid *Pseudolimea duplicata* is one of the most abundant bivalves in the Nusplingen Lithographic Limestone. The specimens are mostly juveniles; the smallest has a length of about 4 mm. The outer shell wears conspicuous radial ribs.

This species can be found occasionally throughout the whole profile. It seems to be rarer or absent only in more clayey parts, probably because of poor preservation conditions. In contrast to *Plagiostoma pratzi*, which is often preserved in calcite, *Pseudolimea duplicata* is only preserved as internal moulds, probably a result of a different shell microstructure or mineralogy. Nearly all specimens are articulated and gaping. Therefore, the bivalves probably died very soon on the sea floor after their entry into the lagoon. In any case, *P. duplicata* represents an allochthonous faunal component.

Remarks. – *Pseudolimea* was probably a byssally attached epifaunal bivalve. Beyond the lithographic limestone facies, the species is extremely rare. Therefore, numerous appropriate habitats must have existed near the Nusplingen lagoon. In the micritic Bankkalk Facies, single valves are more common than articulated specimens.

Genus *Ctenostreon* EICHWALD, 1862

Ctenostreon pectiniforme (SCHLOTHEIM, 1820)
Figs. 3, 13

*1820 *Ostracites pectiniformis*. – SCHLOTHEIM, p. 231.

1975 *Ctenostreon pectiniforme* (SCHLOTHEIM 1820). – YAMANI, p. 72, pl. 4, fig. 4. – [See for extensive synonymy list]

1991 *Ctenostreon pectiniforme* (SCHLOTHEIM). – LAUXMANN, p. 165.

1998 *Ctenostreon pectiniforme* (SCHLOTHEIM 1820). – FISCHER, pl. 1–6.

v 2001 *Ctenostreon pectiniforme* (SCHLOTHEIM). – DIETL & SCHWEIGERT, p. 70, text-fig. 70. – [Nusplingen]

Material: 2 specimens from the Nusplingen quarry, Bed G; comparative material from the Upper Jurassic of the eastern and central Swabian Alb.

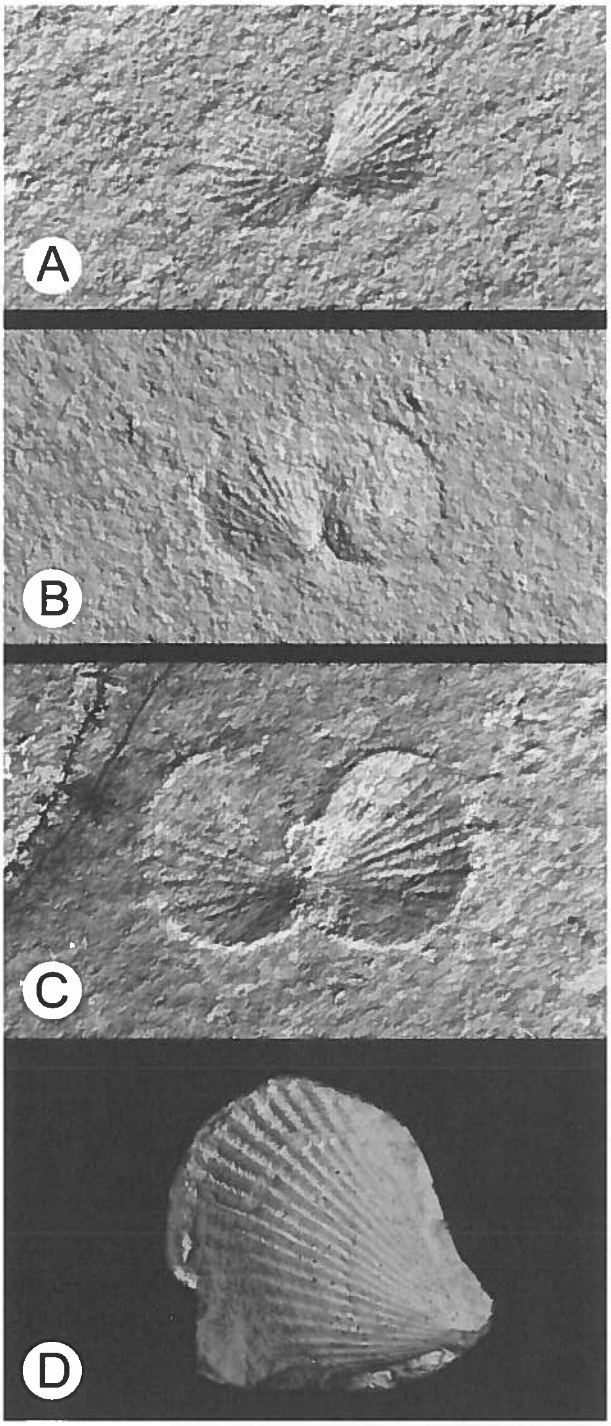

Fig. 12. *Pseudolimea duplicata* (SOWERBY). – **A.** Nusplingen quarry; Nusplingen Lithographic Limestone, Bed G, 20–30 cm below top, lower surface of a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 67347. **B.** Egesheim quarry; Nusplingen Lithographic Limestone, exact bed unknown, lower surface of a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 63246. **C.** Egesheim quarry; Nusplingen Lithographic Limestone, Bed Pk 4, 20–30 cm below top, lower surface of a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 67348. **D.** Steinkern specimen; Herrlingen-Lautern near Ulm; Obere Felsenkalke Formation; Upper Kimmeridgian, Beckeri Zone; SMNS 67349 (leg. BRACHER). – Figs. A–C: × 2/3, Fig. D: × 2.

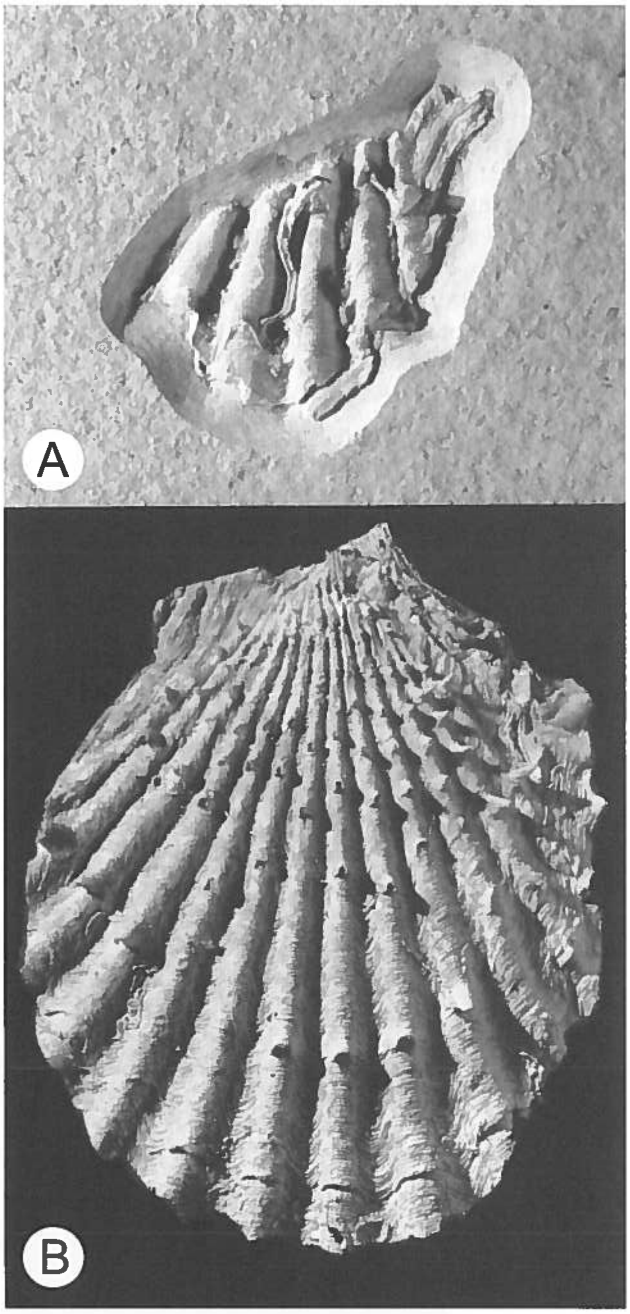

Fig. 13. *Ctenostreon pectiniforme* (SCHLOTHEIM). – **A.** Shell fragment; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed G, 60–70 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 64256. **B.** Silicified specimen; Gerstetten; coral limestone; Upper Kimmeridgian, Ulmense Subzone; SMNS 67350 (leg. KAPITZKE & RIETER 1987). – Fig. A: × 2, Fig B: × 1.

Ctenostreon pectiniforme is only represented by two specimens. One specimen is an isolated shell fragment with coarse ribs (Fig. 13A). It is overgrown with damaged serpulids. The other one is an articulated juvenile specimen (Fig. 3). Both specimens have been assigned to this species by comparing them with complete, silicified specimens from the coral facies of Nattheim and Gerstetten, where *C. pectiniforme* is quite common (Fig. 13B). In contrast, this species is rare in the sponge facies and only known from certain localities. Deposition in this low energy facies can only have occurred as a result of predators. The serpulid overgrowth on the shell fragment (Fig. 13A) had probably been broken by the predator's teeth. Therefore, the overgrowth had to have occurred in the habitat of this species, and not at the place of final burial. However, it is not clear whether the serpulids grew on the shell during the lifetime or after the death of the bivalve.

Remarks. – *Ctenostreon pectiniforme* (SCHLOTHEIM) might represent a younger synonym of *C. proboscideum* (J. SOWERBY) and *C. rugosum* (SMITH) (cf. JAITLY et al. 1995: 178). As there is no current revision of these three species, we assign the specimens described herein to *Ctenostreon pectiniforme* (SCHLOTHEIM).

Family Ostreidae RAFINESQUE, 1815
Genus *Liostrea* DOUVILLÉ, 1904

Liostrea socialis (MÜNSTER in GOLDFUSS, 1829)
Figs. 14–15, 18

*1829 *Posidonia socialis* sp. nov. – MÜNSTER in GOLDFUSS, p. 120, pl. 114, fig. 7.
v 1855 Auster [*Posidonia socialis* GOLDFUSS]. – O. FRAAS, p. 83. – [Nusplingen]
1857 *Posidonia socialis* GOLDFUSS. – QUENSTEDT, p. 801. – [Nusplingen]
1904 Austern. – WALTHER, p. 159. – [Nusplingen]
1911 [Austern]. – STAFF & RECK, pl. 6, fig. 2; pls. 7, 8, 11.
v 1968 *Ostrea socialis*. – LEICH, p. 56, text-fig. p. 57 top.
v 1968 *Ostrea gigantea*. – LEICH, p. 56, text-fig. p. 57 bottom.
1978 "*Inoceramus*" (*Pseudomytiloides*?) sp. – KAUFFMAN, p. 723, text-fig. 3. – [Nusplingen]
1994 *Anomia* sp. – FRICKHINGER, p. 72, text-fig. 83.
1994 *Inoceramus* spec. – FRICKHINGER, p. 74, text-fig. 92.
1994 *Liostrea socialis* (MÜNSTER). – FRICKHINGER, p. 74, text-fig. 93–95.
1994 "*Posidonia*" spec. – FRICKHINGER, p. 76, text-fig. 98.

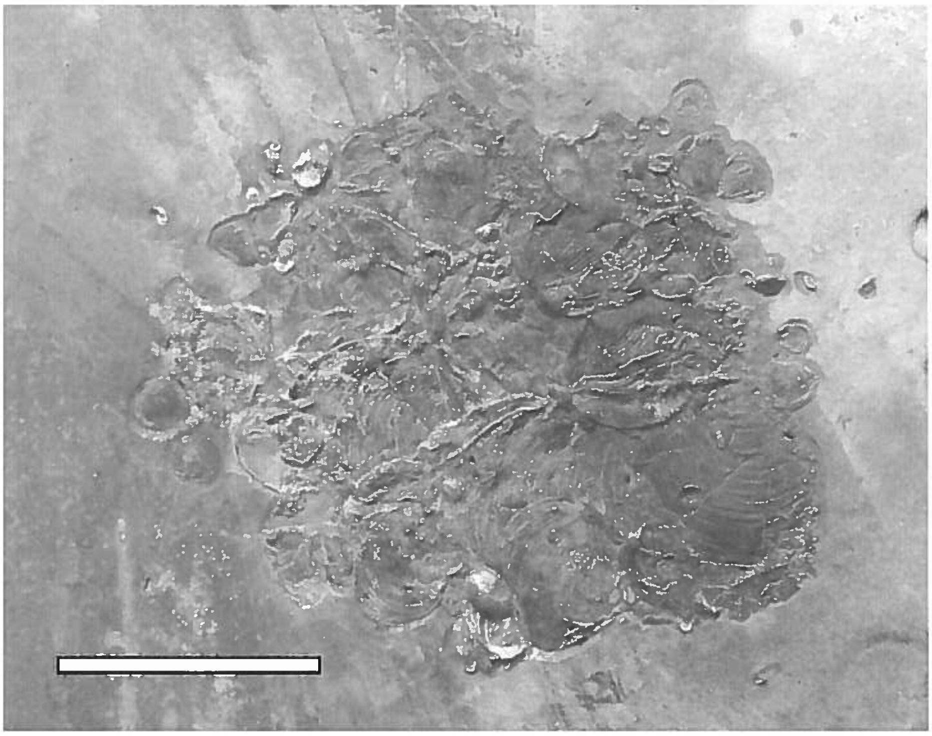

Fig. 14. Accumulation of *Liostrea socialis* (MÜNSTER in GOLDFUSS); Nusplingen quarry; Nusplingen Lithographic Limestone, Bed F, 10–20 cm below top; Upper Kimmeridgian, Ulmense Subzone; SMNS 67351. – Scale: 50 mm.

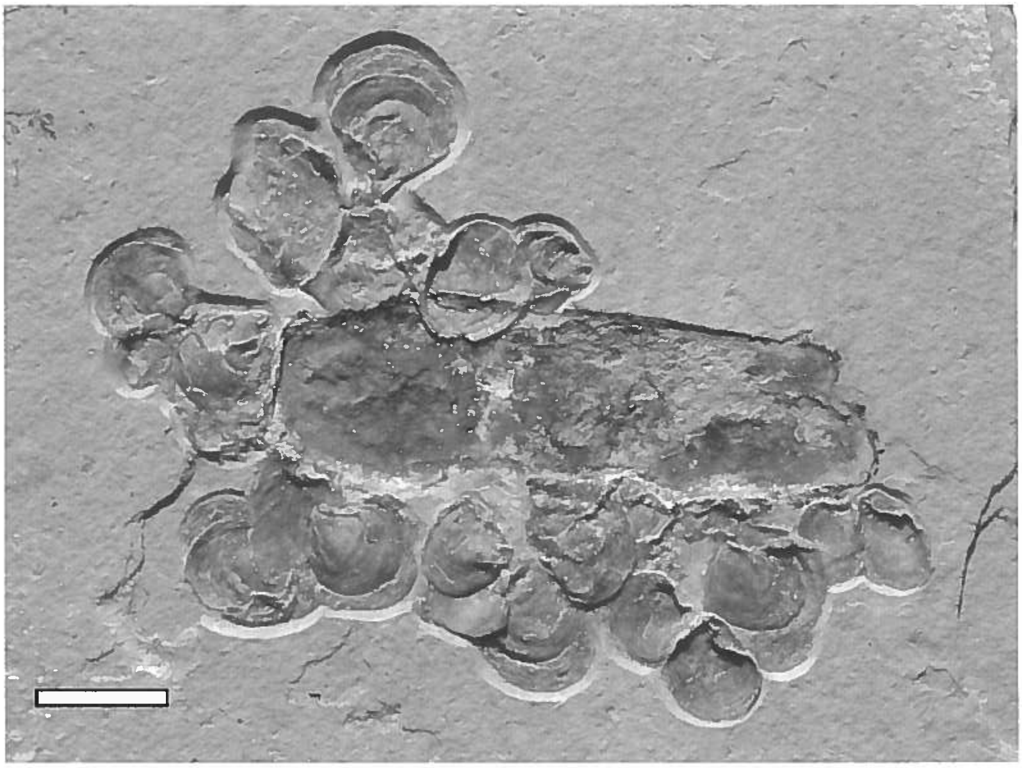

Fig. 15. *Liostrea socialis* (MÜNSTER in GOLDFUSS), overgrowth on a piece of driftwood; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed C, 10–20 cm above K4, upper surface of a layer; SMNS 64539. – Scale: 20 mm.

v 1999 *Liostrea*. – DIETL & SCHWEIGERT, text-fig. 31. – [Nusplingen]
1999 *Liostraea socialis* (MÜNSTER). – KEUPP et al., p. 126, pl. 2, figs. 1, 3–4.
2000 *Liostraea socialis* (MÜNSTER). – RÖPER et al., p. 100, text-fig. 150.
v 2001 *Liostraea socialis* (MÜNSTER). – DIETL & SCHWEIGERT, p. 70, text-fig. 57. – [Nusplingen]
v 2006 *Liostrea socialis* (MÜNSTER in GOLDFUSS, 1835). – VIOHL & ZAPP, p. 73, pl. 4, fig. 4.
v 2007 *Liostrea* sp. – FÜRSICH et al., tables 2–3. – [2007a]
v 2007 *Liostrea* sp. – FÜRSICH et al., pp. 52, 57. – [2007b]
v 2007 *Liostrea socialis* (MÜNSTER in GOLDFUSS, 1835). – VIOHL & ZAPP, p. 135.

Material: More than 500 specimens from the Nusplingen Lithographic Limestone in the quarries of Egesheim, Nusplingen, and the outcrop 'Großer Kirchbühl'; old finds in the collections of the GPIT and the Museum of Natural History of the Humboldt-University in Berlin.

Overgrowth on ammonite conchs consists almost exclusively of the small oyster *Liostrea socialis* (SCHWEIGERT & DIETL 1999). This bivalve was rarely found on isolated phragmocones of belemnites or on juvenile belemnite rostra with adherent phragmocones (SCHWEIGERT 1999), on driftwood (Fig. 15), conifer boughs and scales, sponges of the genus *Codites*, and *Muensteria* worm tubes. Even the thorax region of a dragonfly of the genus *Stenophlebia* was overgrown by some small oysters, which are similar to the specimen described by RÖPER et al. (2000, text-fig. 182) from the laminated limestones of Schernfeld. Contrary to finds from the Posidonia Shale, they do not occur on the exuviae of crustaceans, which suggests short drift times.

Usually, only small, mostly articulated specimens of the species occur in the lithographic limestone facies. Apparently, they could not complete their normal life cycle, as they came into a lethal biotope. In contrast to *Liostrea roemeri* (see below), which has an oblique elongated outline and a pointed umbo, the outline of *L. socialis* is rounded to oval. Very small specimens show a conspicuous concave posterior margin. The smallest specimens are only about 1 mm across, whereas the largest documented specimens are about 3 cm long. Within an accumulation of many specimens, usually all specimens have approximately the same size. Therefore, we assume that they all belong to one generation. Only in very rare cases, for example when attachment occurred during the ammonite's lifetime, several generations are involved in the overgrowth (Fig. 18; see below). However, there are accumulations of *L. socialis* of disparate size (Fig. 14) on the same bedding plane. This suggests various episodes of larval settlement. In *L. socialis*, at least in juvenile stages, allomorphic structures are abundant (cf. WISSHAK et al. 2000).

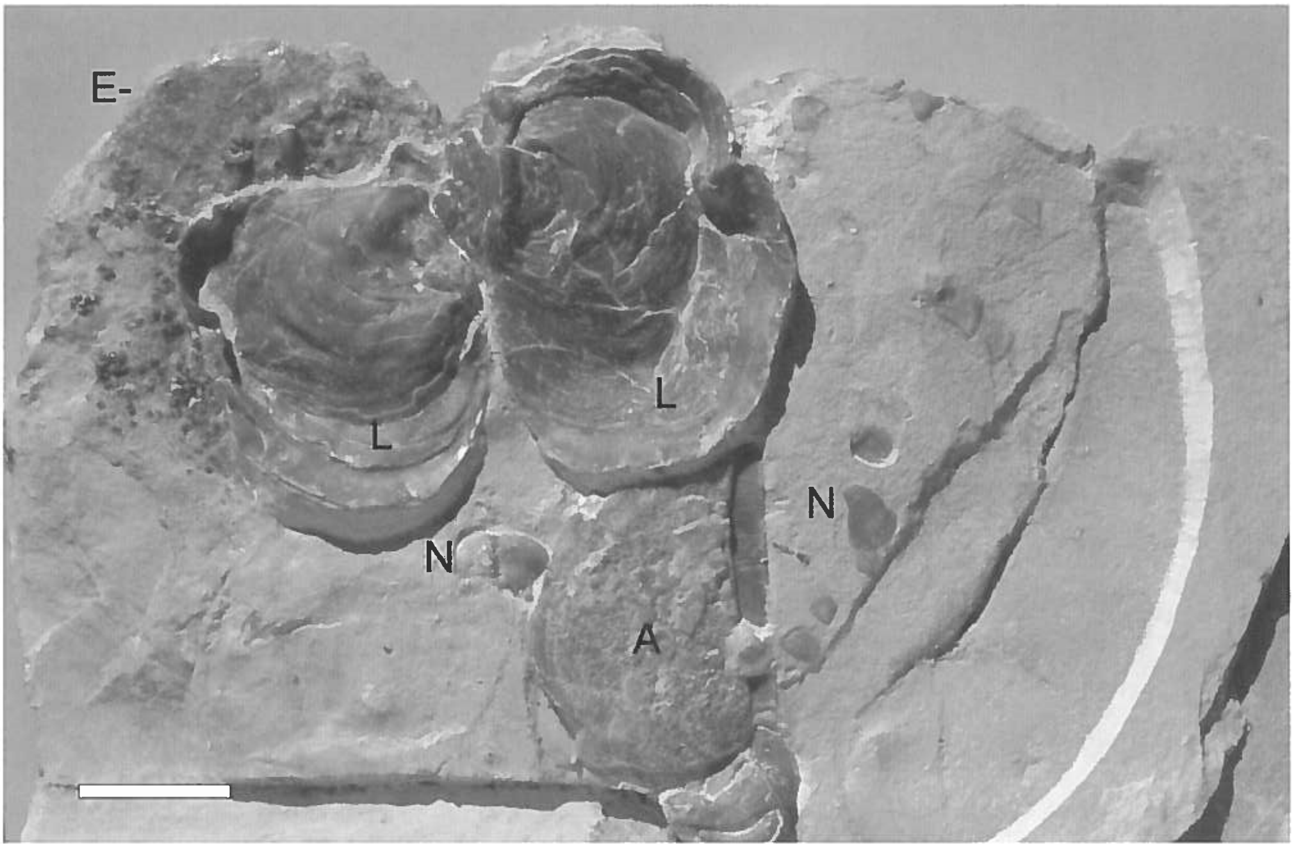

Fig. 16. *Liostrea roemeri* (Quenstedt) (L), *Eopecten velatus* (Goldfuss) (E), and *Nanogyra virgula* (Defrance) (N) growing on the ammonite *Aspidoceras* sp.; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed L, 0–5 cm below top, lower surface of a layer; Upper Kimmeridgian, Ulmense Subzone; SMNS 64381. – Scale: 20 mm.

For example, a left valve from the lithographic limestone of Bed F shows that originally it has been attached to a regular echinoid shell. An allomorphy of perisphinctid shell sculptures in *L. socialis* is even much more common.

Right valves and fragmented valves of *L. socialis* can be often found isolated on bedding planes. Articulated and gaping specimens are much less common. Those isolated specimens might have fallen off disintegrating oyster floats. Occasionally, they also have to be seen as leftovers, what is indicated by broken shells.

Liostrea roemeri (Quenstedt, 1843)
Fig. 16

? 1829 *Posidonia gigantea* sp. nov. – Münster in Goldfuss, p. 120, pl. 114, fig. 4.
*1843 *Ostrea Römeri*. – Quenstedt, p. 434.
v 1856 *Ostrea Römeri*. – Quenstedt, p. 625, pl. 77, fig. 22.
1904 *Ostrea gigantea (Roemeri)* Q. – Walther, p. 169.
1911 [Austern]. – Staff & Reck, pl. 6, fig. 1, pls. 9–10.
1964 *Liostrea roemeri* (Qu.). – Wellnhofer, p. 49.
v non 1968 *Ostrea gigantea*. – Leich, p. 56, text-fig. p. 57 bottom [= *L. socialis*].
v 1996 *Liostrea roemeri*. – Zeiss et al., p. 131, pl. 20.
? 1999 Unbenannte Muschel. – Frickhinger, p. 22, text-fig. 27.
v 2001 *Liostraea roemeri* (Münster). – Dietl & Schweigert, p. 70, text-fig. 126. – [Nusplingen]

Material: Two specimens on an ammonite, few on a further ammonite from the Nusplingen quarry, Bed L; comparative material from the Lower Kimmeridgian Lacunosamergel Formation and the Lower Tithonian Hangende Bankkalke Formation of the Swabian Alb.

This species, which has an elongated shell with an acute umbo ("ham-shaped"), is only represented by a few specimens. Some of them are attached to a large *Aspidoceras* conch. The comparison of this species to *Liostrea socialis* (Goldfuss) from "shell nests" (see above) showed that both species differ significantly from each other already in a juvenile stage.

Liostrea roemeri is a typical overgrowth on ammonite conchs from the Upper Jurassic of Southern Germany. Exhibiting an allomorphic structure, isolated finds mostly turn out to have fallen off oyster floats. As *Aspidoceras* shows nearly no shell sculpture except spines, the encrusting bivalves did not develop an allomorphic shell sculpture. On first sight, the two specimens in the umbilical region of the *Aspidoceras* shell seem to be extremely inequivalve. However, this phenomenon is only caused because both valves experienced compactional distortion.

Genus *Nanogyra* BEURLEN, 1958

Nanogyra virgula (DEFRANCE, 1821)
Fig. 16

*1821 *Gryphaea virgula*. – DEFRANCE, p. 26.
1964 *Exogyra virgula* (DEFRANCE) 1820. – WELLNHOFER, p. 50, pl. 3, figs. 2–7, text-fig. 31. – [See for extensive synonymy list]
1986 *Nanogyra virgula*. – FÜRSICH & OSCHMANN, p. 65.
1991 *Exogyra virgula* (DEFRANCE). – LAUXMANN, p. 165.
v 1995 *Exogyra virgula*. – SCHWEIGERT & SCHERZINGER, p. 316.
1999 *Exogyra* sp. – KEUPP et al., p. 126.
v 2001 *Nanogyra virgula* (DEFRANCE). – DIETL & SCHWEIGERT, p. 70, text-fig. 57. – [Nusplingen]

Material: Clusters of articulated specimens on two ammonites from the Nusplingen quarry, Bed L; numerous comparative specimens from the Hattingen Trümmerkalk Member and the Hangende Bankkalke Formation of the western Swabian Alb, from the uppermost Lower Tithonian Neuburg Formation of southern Franconia, and from the Upper Jurassic of northwestern Germany, England, Switzerland (Canton of Jura), and western France (Boulonnais).

The cementing oyster *Nanogyra virgula* is characterized by a slender, oblique outline, an involute umbo, and radial ribs, which are interrupted by strong growth lines. The largest specimens from Nusplingen are attached to an *Aspidoceras* conch (Fig. 16). As they are embedded below the ammonite shell, both valves of the specimens are preserved. Thus, both valves are preserved in their living position. Other very small specimens of *Nanogyra* have been found together with numerous individuals of *Liostrea socialis* growing on a perisphinctid ammonite, of which the latter oysters show allomorphism.

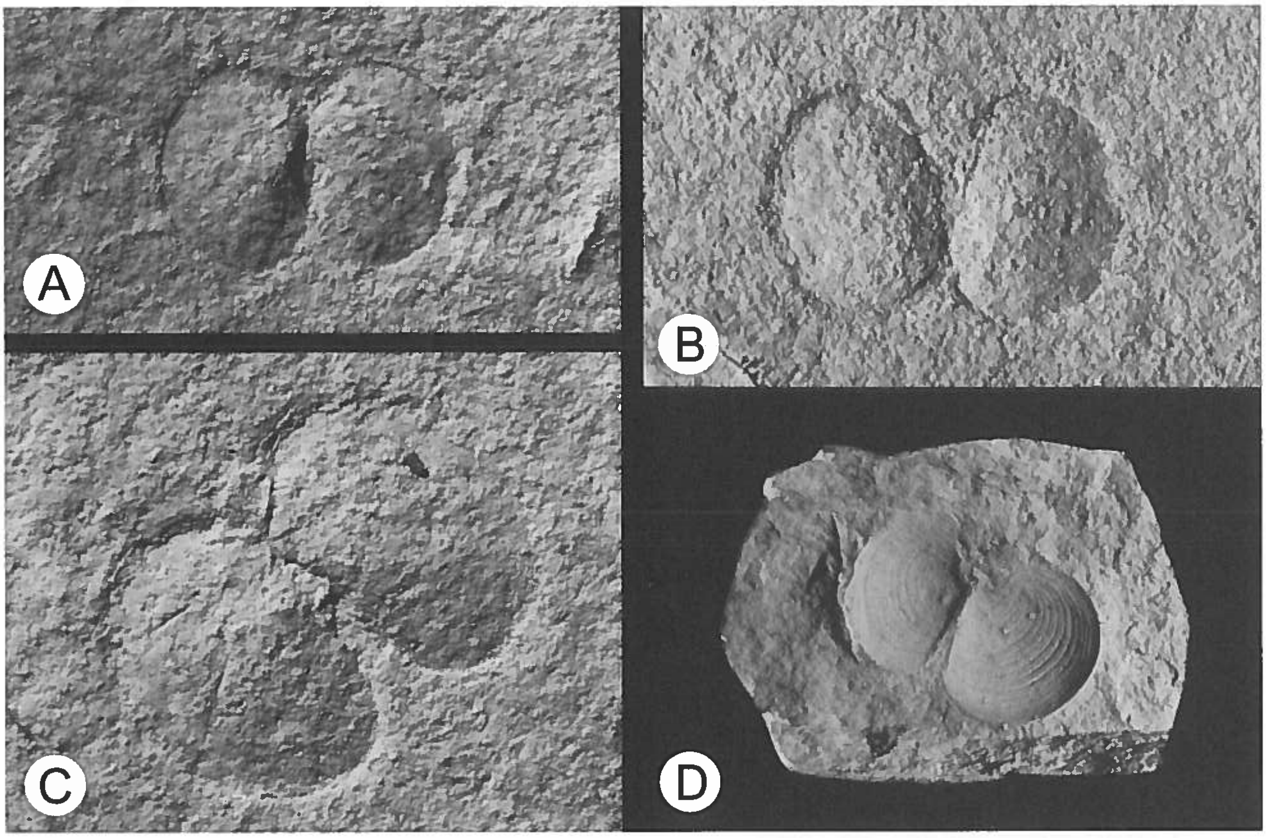

Fig. 17. "*Lucina*" *zeta* QUENSTEDT; Upper Kimmeridgian, Ulmense Subzone. – **A**. Egesheim quarry; Nusplingen Lithographic Limestone, Bed Pk 6, 0–5 cm below top, lower surface of layer; SMNS 67352. **B**. Egesheim quarry; Nusplingen Lithographic Limestone, Bed Pk 4, 0–5 cm below top, lower surface of layer; SMNS 67353. **C**. Cf.-specimen; Egesheim quarry; Nusplingen Lithographic Limestone, Bed Pk 6, 15–25 cm below top, lower surface of layer; SMNS 67354. **D**. Holotype (= QUENSTEDT 1857: pl. 98, fig.18); Ulm-Söflingen; Mergelstetten Formation; IFGT, without number. – Figs. A–D: × 2.

Family Lucinidae FLEMING, 1828

"*Lucina*" *zeta* QUENSTEDT, 1857
Fig. 17A, B, D, ?C

v *1857 *Lucina zeta*. – QUENSTEDT, p. 795, pl. 98, fig. 18. – [Holotype]
v 1908 *Lucina zeta* QU. – ENGEL, p. 473.
1964 „*Lucina*" *zeta*. – WELLNHOFER, p. 77.
? 1985 Bivalve. – BERNIER, p. 66 top.
v 2001 „*Lucina*" *zeta* QUENSTEDT. – DIETL & SCHWEIGERT, p. 70. – [Nusplingen]

Material: More than 20 articulated specimens from various beds of the Egesheim and Nusplingen quarries, all except one embedded in convex-down position; comparative material from the Zementmergel and Mergelstetten formations of the Swabian Alb, including the holotype (Fig. 17D).

The specimens from the Nusplingen Lithographic Limestone which are only preserved as internal moulds agree very well with specimens from strata of nearby contemporaneous environments. The specimens show a conspicuously long lunule. As details of the hinge region are not known, assignment to one of the Jurassic lucinids, such as *Mesomiltha* or *Loripes*, is not possible (cf. WELLNHOFER 1964). "*Lucina*" *zeta* always occurs in "butterfly position". The valves are found in a convex-down position on the bedding plane. The embedding in convex-down position suggests a slow subsidence of the shells in the water column, as it is known from other fossils with convex valves, e. g. terebratulid brachiopods, aptychi, etc. (cf. DIETL & SCHWEIGERT 2000).

"*L.*" *zeta* usually occurs in calcareous marls of the Zementmergel Formation, and as other lucinids has been an infaunal soft sediment inhabitant. An autochthonous occurrence of "*L.*" *zeta* in the Nusplingen Lithographic Limestone is unlikely, as the valves are found isolated on different bedding surfaces, contrary to the mass occurrence of the nuculids described above. Not even burrow tracks were found in connection with the shells. Thus, the specimens from the Nusplingen Lithographic Limestone might have been brought in by predators, which had excavated the bivalves in their original habitat. Some of the shells fell down before they could get cracked. After the death of the bivalve, both valves were held together by the ligament.

A similar or perhaps identical taxon in similar preservation is known from the Lithographic Limestone of Cerin in south-eastern France (BERNIER 1985, text-fig. p. 66 top).

3. Oyster overgrowth and "shell nests"

Finds of "shell nests" are known from the Solnhofen lithographic limestones since MÜNSTER (in GOLDFUSS 1829) and since then are a matter of considerable debate (STAFF & RECK 1911). They were first noticed in the Nusplingen Lithographic Limestone by O. FRAAS (1855: 83) who could not give a thorough interpretation for their occurrence.

ALDINGER (1930: 265) took the oysters for autochthonous benthos. FAHRION (1937) interpreted *Liostrea socialis* as active nekton. As we know today, the latter interpretation is erroneous; although some bivalves (e. g., some pectinids and limids) are able to swim, they can only cover very short distances. Furthermore, after metamorphosis oysters are sessile organisms, most taxa cementing to a hard substrate. The same applies to *Liostrea socialis*, at least in juvenile stages, which can be demonstrated by occasional allomorphic structures (see above).

Oysters of a remarkable size attached to ammonite conchs can be found both in the non-laminated, thicker-bedded facies of the Upper Jurassic and in the Nusplingen Lithographic Limestone. Usually, they may represent a post-mortem phenomenon, particularly when the bivalves grow over the ammonite aperture. The occurrences in the normal bedded facies may represent a post-mortem settlement on the sea floor, which can be recognised by a one-sided growth on the upper side. In the Lithographic Limestone, in contrast, large oysters are restricted to large ammonite conchs, which are very rare in the lagoon. A correspondent case is a macroconch of *Euvirgalithacoceras* sp., overgrown with cirripeds from the Nusplingen Lithographic Limestone (DIETL & SCHWEIGERT 2001, fig. 130.1).

The find of very large representatives of *Liostrea roemeri* growing on an *Aspidoceras* conch, in which the two valves of the Laevaptychus were still lying on top of each other in the body-chamber (Fig. 16), is very astonishing. Probably, the settlement in the umbilical region started when the ammonite was still alive (SCHWEIGERT & DIETL 1999, pl. 3, fig. 1). Furthermore, we found an *Eopecten*, whose cemented valve had been partly overgrown by *Liostrea roemeri* after its death and after the free valve had dropped off. Later, another generation of *L. roemeri* settled on the flanks of the ammonite conch, but only reached a small size. The Laevaptychus stayed apparently in the body-chamber, and seems to have been partly settled by *L. roemeri* at that time. Originally, other representatives of this species were encrusting the shell of the ammonite and were imprinted on the aptychus after dissolution of the shell. Both flanks of the ammonite shell were overgrown with oysters, but the large specimens were only growing in the umbilical region of one flank. Probably because of this unbalance, the ammonite became embedded with this flank lying on the sediment surface. Thus, even after relaxation of the adductor muscles, the valves could not open.

In some cases it could be demonstrated that the shells of living ammonites were overgrown by *Liostrea socialis* (SCHWEIGERT & DIETL 1999). Usually this overgrowth re-

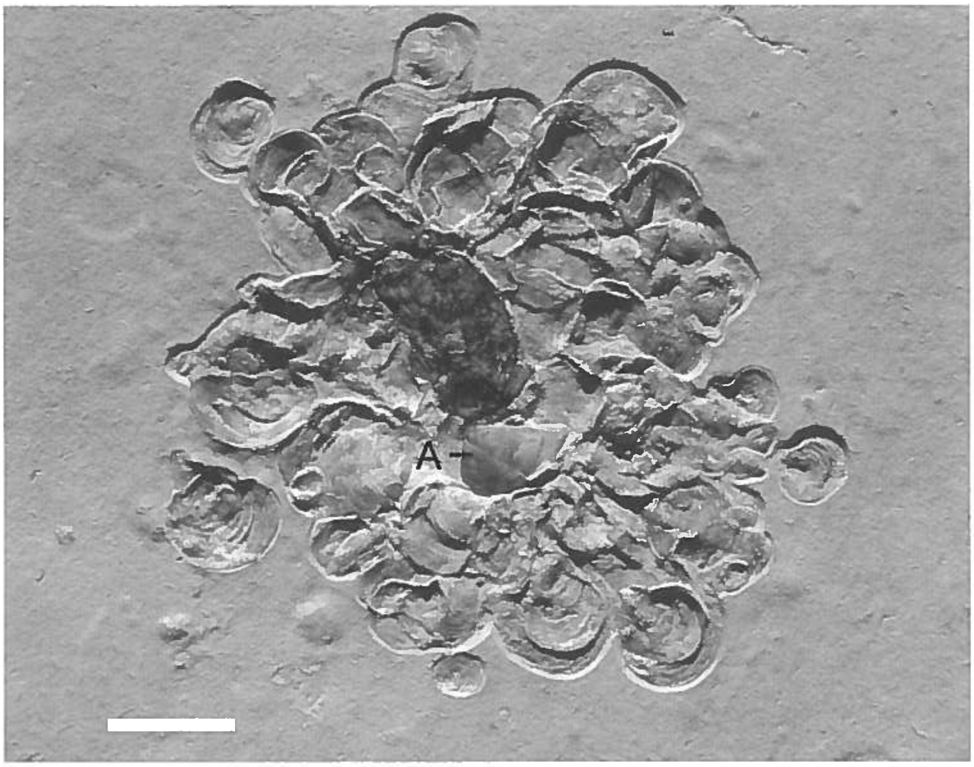

Fig. 18. Two-phase overgrowth of *Liostrea socialis* (MÜNSTER in GOLDFUSS) on living *Physodoceras nattheimense* SCHWEIGERT, the latter showing the Laevaptychus (A) and black organic remains of the soft body; Nusplingen quarry; Nusplingen Lithographic Limestone, Bed D, 10–20 cm below top, upper surface of a layer; SMNS 64428. – Scale: 30 mm.

mained limited to a few small specimens. An exception to this, for example, is a *Physodoceras*, which is preserved with its Laevaptychus and even some organic soft parts, and is overgrown by a huge number of relatively large specimens of *Liostrea* (Fig. 18). Two different size ranges are distinguishable within this oyster overgrowth, which refer to two different settlement stages. The umbones of the oysters point towards the ammonite. Unfortunately, a reconstruction of the bivalve settlement referring to the orientation of the ammonite conch is no longer possible, as the specimen was strongly crushed during diagenesis.

Occasionally representatives of *Liostrea* were growing on ammonite conchs with a broken phragmocone. These ammonites were probably overgrown by *Liostrea* during their lifetime, and were cracked by predators. The conch and its overgrowth then sank down on the lagoonal floor, as it had lost its ability to float.

In contrast, some "shell nests" can be without doubt interpreted as remains of meals, as the broken shells show no preferred orientation. Other fossils, e. g. small belemnite rostra or numerous ammonites, can also be involved in these "shell nests" (Fig. 14). In one case, the accumulation consists of several perisphinctids and only few small oysters; in another case of numerous oppeliids and a slight oyster overgrowth. However, even in layers with a high organic carbon content, no algal remains were found on these objects although algae are preservable in these layers (SCHWEIGERT 2001). Presumably these ammonites and belemnites with their overgroth have been taken up by a predator in the water column. KEUPP (2002) interpreted similar accumulations from the Solnhofen lithographic limestones as rafts bound by drifting sponges (*Codites* ssp.), but among the material from Nusplingen, there is not a single example in which sponges are involved.

Thus, the origin of a "shell nest" has to be analysed in every single case, and cannot be generalised. In the majority, the prepared materials represent remains of meals. Until now, no indications have been found in the Nusplingen Lithographic Limestone confirming KAUFFMAN's (1978) idea of "benthic islands". In the Lower Jurassic Posidonia Shale, the bulk of bivalves growing on ammonite conchs has been interpreted as representing a pseudoplanktic life style (SCHMID-RÖHL & RÖHL 2003). They also interpreted ammonite conchs lying on the seafloor and overgrown with numerous bivalves from the Posidonia Shale as a post-mortem colonization. Concerning some examples from the Nusplingen Lithographic Limestone, this interpretation seems to be questionable. Obviously, the uplift of an ammonite conch could compensate a considerable additional weight produced by bivalve overgrowth, both in living animals and in empty, drifting conchs.

4. Palaeoecology

The seafloor of the Nusplingen lagoon was apparently not suitable for an infaunal settlement of bivalves, although its substrate had basically the same composition as the limestones of the Bankkalk Formation of the same age. A monospecific nuculid population did exist only during one short period, although these bivalves were shallowly burrowing soft-substrate dwellers. Before the bivalves had reached their adult size, almost the entire generation died off. Only a small percentage survived one further, short-time sedimentation event. Similar to the monospecific layer of *Polycidaris nusplingensis* documented in the same profile, the nuculids died because of anoxic conditions on the sea floor (cf. GRAWE-BAUMEISTER et al. 2000), and not because the texture of the substrate was unsuitable.

Autochthonous epifaunal hard substrate dwellers are completely missing in the Nusplingen Lithographic Limestone (Tab. 1), even though secondary hardgrounds such as belemnite rostra or ammonite conchs were abundant. In most cases, larger objects such as belemnite rostra or ammonite conchs could not sink into the substrate completely and protruded partly over the sediment surface, depending on the consistency of the substrate. The interpretation of accumulations of oysters on such hardparts as short-lived benthic communities (so-called "benthic islands"; KAUFFMAN 1978) could not be substantiated in all cases studied so far.

In the Nusplingen Lithographic Limestone, only a small population of small nuculids represent typical r-strategists, according to their monospecific mass occurrence. Representatives from other Jurassic fossil sites from southwest Germany are for example *Bositra* and *Pseudomonotis* from the Posidonia Shale in the Swabian Lower Jurassic, or *Aulacomyella ("Pseudomonotis") similis* (QUENSTEDT), a low-oxygen specialist from the Lower Kimmeridgian Lacunosamergel Formation. *Aulacomyella* has also been reported from the plattenkalk of Wattendorf in northern Franconia (FÜRSICH et al. 2007a, b). Above and below the nuculid beds, slightly bioturbated layers containing *Spongeliomorpha* (= "*Thalassinoides*"), *Rhizocorallium*, *Parahaentzschelinia* etc. occur. This implies that living conditions were more suitable during these times. Other bedding planes in this limestone section show raised, irregular polygonal structures, which we interpret as microbial mats, but they were apparently not grazed.

Besides brachiopod shells, bivalve shells are a subordinate biogenic component of the coarse fraction in turbidite beds of the Nusplingen Lithographic Limestone. Normally, the specimens cannot be assigned to a certain species because of their fragmentation. Only *Chlamys textoria* (see above) could be identified in such a turbidite layer.

Tab. 1. List of the described bivalve species from the Nusplingen Lithographic Limestone, and their presumed life habitats.

Species	Relation to the lithographic limestone	Life style	Number of specimens
Nuculidae gen. et sp. indet.	autochthonous	shallow infaunal	(numerous)
Nuculana (Rollieria) sp.	allochthonous	shallow infaunal	1
Arca (Eonavicula) cf. *fracta*	allochthonous	byssally attached	2
Pinna sp.	allochthonous	endobyssate	1
Propeamussium nonarium	allochthonous	byssally attached	1
Chlamys textoria	allochthonous	byssally attached	1
Camptonectes auritus	allochthonous	byssally attached	2
Cingentolium cingulatum	allochthonous	? byssally attached	1
Eopecten velatus	allochthonous	cemented	2
Spondylopecten palinurus	allochthonous	byssally attached	1
Radulopecten sigmaringensis	allochthonous	byssally attached	1
Plagiostoma pratzi	allochthonous	byssally attached	5
Pseudolimea duplicata	allochthonous	epifaunal byssate	>30
Ctenostreon pectiniforme	allochthonous	byssally attached	2
Liostrea socialis	allochthonous	cemented, optionally pseudoplanktic	>500
Liostrea roemeri	allochthonous	cemented, optionally pseudoplanktic	<10
Nanogyra virgula	allochthonous	cemented, optionally pseudoplanktic	<10
"Lucina" zeta	allochthonous	deep infaunal	>20

5. Comparisons with other lithographic limestone deposits

As habitats with many benthic organisms were located nearby the Nusplingen lagoon, the number of taxa documented in the Nusplingen Lithographic Limestone is relatively high compared with that of other lithographic limestone deposits. Considering the number of finds, only representatives of the genera *Liostrea* and *Nucula* play an important role in the Nusplingen Lithographic Limestone. This kind of distribution is also found in the lithographic limestones of Solnhofen and Eichstätt. Comparable bivalve faunas that are autochthonous, mostly monospecific, or of low diversity, also exist at other localities in Bavaria such as Brunn near Regensburg (Röper et al. 1996), Hienheim near Kelheim (Röper & Rothgaenger 1998), or Pfalzpaint (Röper et al. 1999). In comparison to the Nusplingen Lithographic Limestone, no nuculids are found at these localities. In contrast, *Solemya*, a bivalve from the Bavarian deposits, which usually is associated with typical burrows, is completely missing in the Nusplingen Lithographic Limestone.

Other rare, mostly allochthonous bivalve species from Franconian lithographic limestones (e. g. Barthel 1978; Frickhinger 1994, 1999) also occur in the Nusplingen Lithographic Limestone. Further excavations in the Nusplingen Lithographic Limestone will probably increase the diversity of allochthonous bivalve species known so far from adjacent biotopes.

Besides *Liostrea* and barnacles, *Nanogyra* is a very common encruster in the plattenkalk deposit of Brunn near Regensburg in eastern Bavaria (Keupp et al. 1999). *Nanogyra* is extremely rare in the Nusplingen Lithographic Limestone, but is very abundant in higher energy deposits of the SW Swabian Alb and the northern Hegau, e. g. in the Hattingen Member, and can be found in this region up to the Hangende Bankkalk Formation of the Lower Tithonian (Schweigert & Scherzinger 1995: 316). As the few specimens from Nusplingen presented herein are quite large, they probably drifted for a long time on the ammonite conch on which they are preserved. A comparable specimen of the Tethyan ammonite species *Phylloceras* cf. *saxonicum* encrusted with *Nanogyra virgula* was found in the Upper Jurassic coral limestone of Gerstetten (E Swabian Alb) (Rieter et al. 2000). Possible reasons for the rareness of *Nanogyra virgula* might be the unavailability of suitable habitats nearby the laminated limestone lagoons or the occupation of its ecological niche by *Liostrea*.

6. Future prospects

Compared with other lithographic limestone deposits, the bivalve fauna of the Nusplingen Lithographic Limestone is surprisingly rich, although most taxa are only represented by single finds (Table 1). This clearly shows the allochthonous character of the bivalve fauna. As time-equivalent deposits near Nusplingen have been eroded, the allochthonous faunal elements are very important for obtaining information about these eroded strata. Presumably, more taxa will be found at further excavations in the Nusplingen Lithographic Limestone. The statistical distribution of the taxa is largely subject to chance because of their allochthonous character. Therefore, such an analysis has not been carried out. For an exact reconstruction of nearby habitats on the basis of benthic assemblages, the in-situ assemblages of the coral limestones, for example, have to be analysed and characterised with respect to their composition first. However, similar investigations in the Upper Jurassic of South Germany are still missing.

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