A multidisciplinary study of Late Jurassic bivalves from a semi-enclosed basin – Examples of adaptation and speciation and their stratigraphic and taphonomic background (Lusitanian Basin, central Portugal)

Dissertation zur Erlangung des Doktorgrades (Dr. rer. nat.)
an der Fakultät für Geowissenschaften
der Ludwig-Maximilians-Universität München

vorgelegt von

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im September 2009

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Tag der mündlichen Prüfung: 13.01.2010

Ehrenwörtliche Versicherung

Ich versichere hiermit ehrenwörtlich, dass die Dissertation von mir selbstständig, ohne Beihilfe angefertigt worden ist.

München, 15.09.2009

Erklärung

Hiermit erkläre ich, dass die Dissertation noch nicht in einem anderen Prüfungsverfahren vorgelegt und bewertet wurde.
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München, 15.09.2009

Contents

1. Introduction

This thesis summarises the results of four years of research on more than 2200 bivalve specimens from Upper Jurassic strata of the Lusitanian Basin in central Portugal. The Lusitanian Basin is a semi-enclosed rift basin of approximately 50,000 km^2 in size that was situated at the eastern margin of the Proto-Atlantic Ocean during the Mesozoic. During the Late Jurassic, the connection to the open sea was limited to the southern end of the basin. Therefore, the Lusitanian Basin represents an excellent object to study the faunal evolution in a geographically confined marginal marine area across a time span of at least 15 Ma. Prior to the Middle Oxfordian, when the major Late Jurassic transgression took place and flooded the area, the Lusitanian Basin was exposed to erosion. Consequently, the development of the Late Jurassic marine fauna of the basin can be studied right from the time of colonisation in the Middle Oxfordian up to its termination due to infilling of the basin in the Late Tithonian. From its initial break-up until modern times the Lusitanian Basin occupies an intermediate position between the Boreal and Tethys (Mediterranean) biogeographic realms and any biological input may have originated from both regions. Last not least, unique, highly fossiliferous outcrops are exposed along the Atlantic coast, which is subject to erosion and therefore permanently sets free new fossil material. Additionally, large parts of the countryside are occupied by agricultural areas and, due to a building boom during the last decade, a number of artificial outcrops that could be intensely sampled existed.

Prior to the strictly palaeontological part of the present studies, the sampled localities had to be dated as accurate as possible. The semi-enclosed nature of the basin, which is a blessing for detailed bivalve studies, is a curse for biostratigraphy, as ammonites are virtually absent from most strata. Due to the gradual infilling of the basin from the north, lithostratigraphic units are largely diachronous. Moreover, lithostratigraphy suffers from various competitive classification schemes. In order to at least partly avoid these difficulties, the lithostratigraphy was updated and a uniform scheme for the entire Lusitanian Basin was developed. However, some of the units used herein still need to be formalised by the selection of type sections. For a large number of localities representing most of the lithostratigraphic units Sr-isotope ages were calculated. Mainly, different oyster shells were used for the analyses as these organisms are common in most strata and mineralise a primarily calcitic shell which remains relatively stable during diagenesis (SCHNEIDER et al. in press).

Bivalves comprise the most abundant group of macrofossils in most of the Upper Jurassic strata of the Lusitanian Basin, both with regard to diversity and richness. Moreover, bivalve shells are ideal subjects for studies on the interplay of organisms and habitat for several reasons. On one hand, bivalves are known to be sensitive to environmental parameters and record changes in environment directly in their shells. Partially, these modifications can be observed from morphology (e.g., facies, water energy, competition for space or food availability). Additionally, the chemical composition of the shells, especially the values of certain stable isotopes, may vary depending on fluctuations in water temperature and salinity, and may thus be analysed to reconstruct these parameters. On the other hand, evolutionary changes in bivalves appear to occur relatively slowly in most cases. This may be either due to low evolutionary rates or general difficulties in detecting these changes, as most bivalve shells show only few distinctive characters (AMLER et al. 2000). As one consequence, bivalves are rarely useful for biostratigraphy. Despite of these adverse conditions, the main goal of the present work is to detect morphologic phylogenetic trends and changes among several bivalve target taxa during the Late Jurassic and to clearly distinguish these evolutionary patterns from reversible morphologic changes referable to ecophenotypism. The target taxa were chosen because of their frequency both in time and space and/or their obvious shape variability. In many cases, these and other taxa accumulated in shell concentrations in the Lusitanian Basin. The mode of their formation and their palaeoecological and sequence stratigraphic background have been analysed, as taphonomic parameters offer interesting clues on bivalve life in the respective habitats (FÜRSICH et al. accepted).

Besides its regional importance for the understanding of ecosystems in the Upper Jurassic of the Lusitanian Basin and the role of bivalves within them, the present study also offers a global perspective. At least since the Late Palaeozoic, bivalves are one of the dominant groups of benthic invertebrates and display a remarkable diversity. In order to utilise bivalves for issues of palaeobiodiversity, palaeobiogeography or palaeoecology, the initial and essential step is a correct identification of species. However, in contrast to many Cenozoic representatives, most of the Mesozoic and Palaeozoic bivalve groups still suffer from over-splitting, and modern species concepts that pay attention to intraspecific variability are lacking. Partially, this is surely a matter of preservation, as bivalves from these epochs often are preserved as moulds. In the present compilation, case studies on representatives of several bivalve families that are common in Mesozoic shallow marine ecosystems have been carried out, and modern species concepts have been developed using classic taxonomy and morphometric techniques. As a future perspective, these concepts may be extrapolated to other regions, strata or taxa, and may lead to comprehensive taxonomic revisions of bivalve families. These data form a solid base for comprehensive research in the disciplines mentioned above, and the results on the taxa from Portugal have been interpreted with regard to palaeoecology, ecophenotypy, phylogeny and partially alsoontogeny and palaeobiogeography.

Abbreviations used in the text:

AAS = Atomic Absorption Spectrometry
BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, Munich
CLB = central Lusitanian Basin
DEES = Department of Earth and Environmental Sciences, Ludwig-Maximilians-University, Munich
FFT = Fast Fourier Transformation
IGM = Instituto Geologico e Mineiro, Lisbon
NLB = northern Lusitanian Basin
PCA = Principal Component Analysis
SLB = southern Lusitanian Basin

2. Study area

The Lusitanian Basin stretches along the western margin of central Portugal and extends for approximately 300 km in length and 180 km in width including the shelf areas (Fig. 1) (e.g., BOILLOT et al. 1973, 1974, 1975; MONTENAT et al. 1988; HILL 1989). Onshore, the Lusitanian Basin reaches from Aveiro in the north to the Serra d'Arrabida south of the Tagus River. To the east it is bordered by basement rocks of the Iberian Meseta. To the west crystalline remnants of the former basin margin can be found on the Berlenga Horst (CARVALHO et al. 2005).

Structurally, the Lusitanian Basin is an evaporite-prone rift-basin situated at a passive continental margin and developed during three major rifting phases in the Triassic, the Sinemurian to Pliensbachian and the Late Oxfordian, the latter marking the phase of main subsidence (e.g. WILSON 1975; WILSON et al. 1989; ALVES et al. 2002, 2006). A fourth rifting phase occurred west of Iberia during the Early Cretaceous. The basin is partitioned into three sectors by a set of major faults of supposed Variscan origin (CARVALHO et al. 2005). As early as in the Triassic, the basin was divided in a northern and southern part by the Nazaré Fault. Subdivision continued in the southern sector, resulting in a central part situated between the Nazaré and Tagus faults, and a southern part limited by the Arrábida fault.

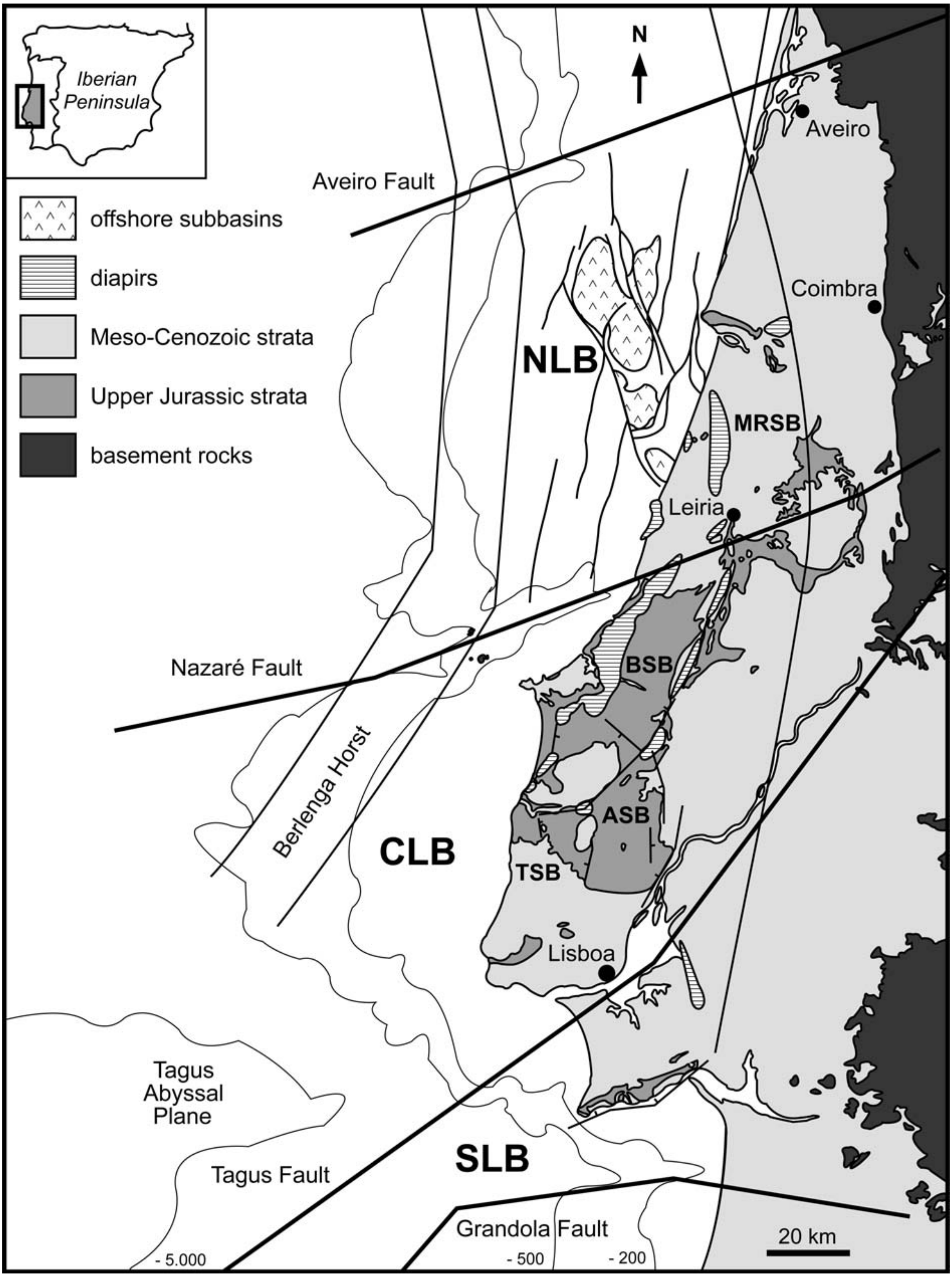

Fig. 1. Geologic overview showing onshore and offshore parts of the Lusitanian Basin as far as recognized by seismic mapping. NLB = northern Lusitanian Basin; CLB = central Lusitanian Basin; SLB = southern Lusitanian Basin; MRSB = Monte Real Subbasin; BSB = Bombarral Subbasin; ASB = Arruda Subbasin; TSB = Turcifal Subbasin.

During the Late Jurassic, partitioning into different subbasins started, when the rise of salt domes along lineaments of Variscan origin was triggered by rapid rifting. In the northern Lusitanian Basin (NLB), five off-shore Late Jurassic sub-basins have been detected based on seismic and well data (ALVES et al. 2002). Onshore, the northernmost **Monte Real Subbasin** is separated from the central Lusitanian Basin (CLB) by the Berlenga-Santarem structural high (TRESNIOWSKI 1958), which is positioned along the Nazare Fault. The CLB is partitioned into at least three sub-basins (ALVES et al. 2003). (1) The **Bombarral Subbasin** is bordered to the south and east by the Torres Vedras-Montejunto High. To the north and west, it is separated from the coastal regions by the Caldas da Rainha, Obidos, Bolhos, and Vimeiro diapirs, and the Serra d'El Rei tectonic high in between. (2) The **Arruda Subbasin** is delineated by the Vila Franca Fault to the southeast, the Runa Fault to the west, and the Torres-Vedras-Montejunto High to the north. (3) The **Turcifal Subbasin** lies south of the Torres Vedras Fault and west of the Runa Fault. Its western margin is drowned in the Atlantic. South of the Vila Franca Fault the **Lower Tagus Subbasin** (= southern Lusitanian Basin, SLB) is largely overlain by Cenozoic strata, and has therefore been explored mainly by drilling. Outcrops of Jurassic strata exist in the Serra d'Arrábida, which marks the southern margin of the Lusitanian Basin along the Arrábida Fault. For the CLB and SLB, seismic and well data do not provide significant information on further palaeogeographic subdivision of the Upper Jurassic strata in the off-shore area (BOILLOT et al. 1975; ALVES et al. 2006). Although the **coastal parts between the Nazaré and the Torres Vedras faults**, which are located at the western flanks of the diapir chain cannot be directly linked to one of the subbasins, these successions may be interpreted as marginal facies of corresponding structures to the west.

3. Lithologic and stratigraphic overview

The Upper Jurassic strata in the Lusitanian Basin formed during a single megasequence and comprise a total thickness of approximately 2700 m (ALVES et al. 2002, 2006). As the entire Lusitanian Basin dips to the SSW, the transition from marine to terrestrial sedimentation associated to the infilling of the basin and/or regression during the Late Jurassic gradually prograded southwards, which is expressed by several large-scale, diachronous lithostratigraphic units. Continuous marine sedimentation from the Oxfordian to the Cretaceous only occurred in the southwestern part of the basin. The lithostratigraphic subdivision of Late Jurassic strata used herein is largely adapted from RASMUSSEN et al. (1998), with partial replacement of terms and further refinement. Formations and members in small letters have not yet been formally established. An overview on terms and current stratigraphic interpretation is given in Figure 2. The Oxfordian-Kimmeridgian stage boundary is interpreted *sensu gallico* herein (MELÉNDEZ & ATROPS 1999). The subdivision of the Kimmeridgian follows ENAY (1997).

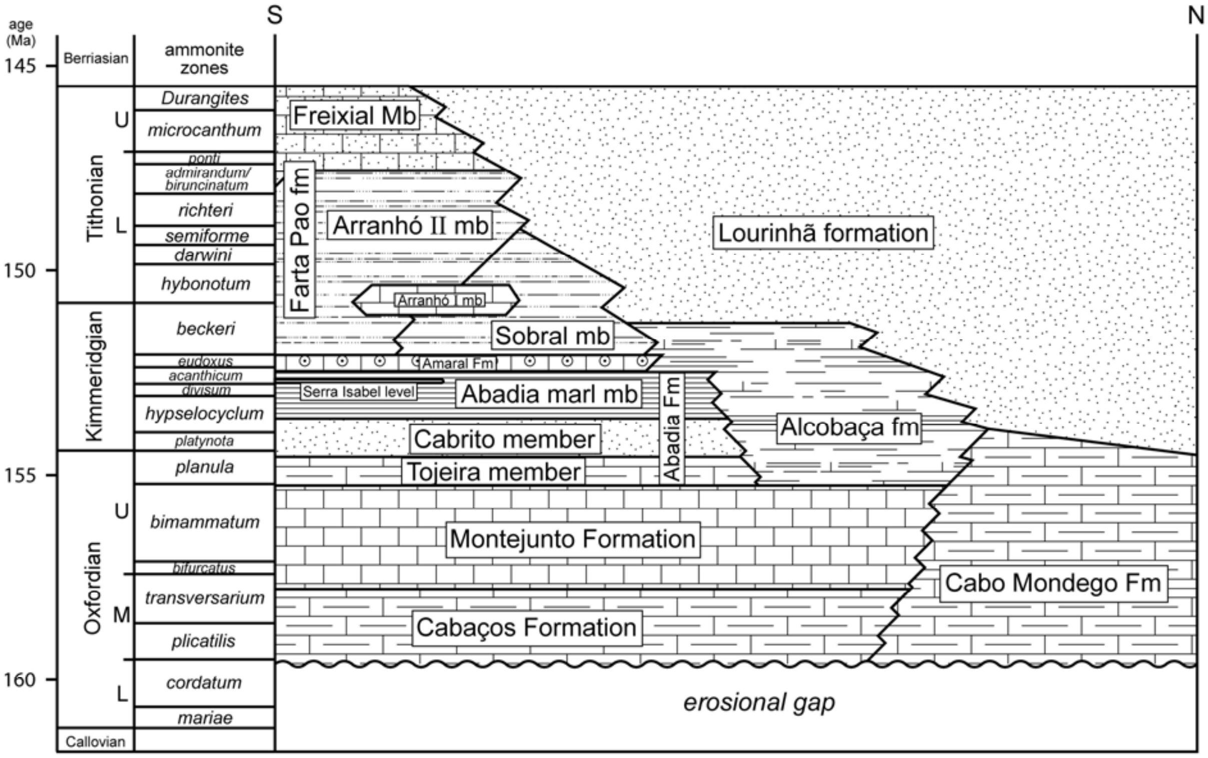

Fig. 2. Lithostratigraphy of the Upper Jurassic rock succession of the Lusitanian Basin. Note that several of the stratigraphic units have not yet been formalized and are therefore written in small letters (modified from SCHNEIDER et al. in press).

After an erosional gap produced during a regressional phase in the Bathonian-Late Callovian/Early Oxfordian (MOUTERDE et al. 1979; AZEREDO et al. 2002), the sedimentation in the Late Jurassic started in the ?latest Early/Middle Oxfordian all across the Lusitanian Basin (AZEREDO et al. 1998, 2002). In the SLB and CLB, the **Cabaços Formation**, introduced as a lithostratigraphic unit by CHOFFAT (1893b), marks the onset of the Oxfordian transgression. The type section is situated in the vicinity of Torres Vedras (MOITINHO DE ALMEIDA et al. 1958). Deposition started with lacustrine to brackish-water calcareous mudstones (ELLIS et al. 1990) which were, due to the absence of sound stratigraphic markers, assigned to the Middle Oxfordian only by the occurrence of the dasycladacean *Heteroporella lusitanica* (RAMALHO 1971b; PEREIRA et al. 2003). Sr isotope data from the basal part of the Cabaços Formation at the Cesareda-Serra d'El Rei plateau suggest a Middle to Late Oxfordian age (SCHNEIDER et al. in press). In the southern part of the basin (e.g. in the type region) the upper part of the unit is composed of marine marly limestones and can be placed in the Middle Oxfordian based on ammonites (RUGET-PERROT 1961).

The Cabaços Formation is conformably overlain by the marine calcareous **Montejunto Formation** introduced by CHOFFAT (1893b). The type section is situated north of Cabanas de Torres, immediately W of Montejunto (CAMARATE FRANÇA et al. 1964a, b; GOMES 1962). These limestones are dated as late Middle to Late Oxfordian by ammonites (RUGET-PERROT 1961, ATROPS & MARQUES 1988a). No calcitic fossils from the Montejunto Formation were available for isotope studies.

In the NLB, both Cabaços and Montejunto formations are replaced by the **Cabo Mondego formation** (WITT 1977; RASMUSSEN et al. 1998), which was regarded part of the Cabaços Formation by AZEREDO et al. (1998, 2002) and AZEREDO & CABRAL (2004). However, the Cabaços Formation as a whole is predominantly calcareous and formes a transgressive sequence tract. In contrast, the Cabo Mondego formation is composed of a heterogeneous, siliciclastic-influenced series of carbonates, marls, and anhydrites (ALVES et al. 2002) indicating an overall regressive tendency and a more proximal setting, since gradual infilling in the NLB had started already at this early stage. In the type section at Cabo Mondego (see RUGET-PERROT 1961, WITT 1977, WILSON 1979, and AZEREDO et al. 1998, 2002 for details), the Middle/Late Jurassic unconformity is directly followed by fossiliferous sandstones containing oysters and oyster-coral patch reefs. Sr isotope values from these oysters indicate a Middle Oxfordian age, while data from higher up in the section range to the Early Kimmeridgian (SCHNEIDER et al. in press).

All over the Lusitanian Basin the Oxfordian-Kimmeridgian transition is characterised by an abrupt change from calcareous to siliciclastic sedimentation initiated by a major rifting event (e.g., WILSON 1979; LEINFELDER & WILSON 1998). Subsequently, three lithological units replace each other in north-south direction during the Late Oxfordian to early Late Kimmeridgian.

In the SLB and large parts of the CLB, the **Abadia Formation**, introduced by CHOFFAT (1885, 1887), mainly comprises turbiditic sandstones and deep-water marls as can be observed at the type section in the Abadia valley (ZBYSZEWSKI 1965). In the Montejunto area, the basal Upper Oxfordian Tojeira member (cf. MOUTERDE et al. 1973; ATROPS & MARQUES 1988a; LEINFELDER & WILSON 1998), is still calcareous but characterized by an increase of fine-clastic sediment. This unit is followed by coarse-grained conglomerates and sandstones of the Cabrito member and finally by the Abadia marls (MOUTERDE et al. 1973). Approximately 40 m below the top of the formation local crinoid-coral-algal build-ups form the Serra Isabel level that has been dated to Lower to Upper Kimmeridgian (SCHNEIDER et al. in press), while a middle Upper Kimmeridgian age had been assumed for the top of the Abadia Formation (LEINFELDER 1993; LEINFELDER & WILSON 1998; LEINFELDER et al. 2004; SCHMID & WERNER 2005).

In the CLB the **Amaral Formation** directly rests on the Abadia Formation. In large areas this unit is composed of shallow marine oolites and sandstones, i.e. the former *Lima pseudalternicosta* beds (CHOFFAT 1901; HILL 1989). Especially in the Arruda Subbasin these facies are replaced by coral limestones, i.e. the Corallien d'Amaral of CHOFFAT (1893b). A type section of this facies was published by ZBYSZEWSKI (1965). No calcitic fossils were available for isotope dating, but based on microfossils and ammonites, a Late Kimmeridgian age is assumed for the Amaral Formation (ELLIS et al. 1990; LEINFELDER & WILSON 1998). North of Bombarral, the Abadia and Amaral formations are replaced by the **Alcobaça formation** introduced by CHOFFAT (1885-88), a heterogeneous succession of marginal-marine, brackish and terrestrial limestones and siliciclastics (CAMARATE FRANÇA & ZBYSZEWSKI 1963). Traditionally, the Alcobaça formation is thought to span (almost) the entire Kimmeridgian (e.g., RUGET-PERROT 1971; WITT 1977; WILSON 1979; FÜRSICH & WERNER 1986; RASMUSSEN et al. 1998; ALVES et al. 2002). However, the unit seems to be slightly older than initially thought. Foraminifers from the coastal section of Salgados (FATELA 1990) and Sr isotope data from several localities (SCHNEIDER et al. in press) indicate a latest Oxfordian to Late Kimmeridgian age. According to HELMDACH (cited in FÜRSICH & WERNER 1991), the ostracod fauna also points to an early Late Kimmeridgian age for the top of the Alcobaça formation. Based on ammonites MARQUES et al. (1992) dated the top of the formation as Early Tithonian. However, Sr isotope data from the uppermost part of the respective section at Vestiaria indicate a Late Kimmeridgian age (SCHNEIDER et al. in press).
The fluvial sandstones of the **Lourinhã formation**, i.e. the "grès supérieurs" of CHOFFAT (1882) or "grés superiores com vegetais e dinosáurios" of ZBYSZEWSKI & MOITINHO DE ALMEIDA (1960), were deposited contemporaneously with the Abadia and Alcobaça formations in the northernmost sector of the basin. With time, the Lourinhã formation (*sensu* HILL 1989; including the Bombarral formation of LEINFELDER & WILSON 1989 and MANUPELLA 1998) gradually expanded southward and finally covered the entire NLB and large parts of the CLB. Stratigraphically, the unit spans the Kimmeridgian and Tithonian as a whole (cf. TEIXEIRA 1948, 1950; HELMDACH 1971b, 1974; RAMALHO 1971a; WITT 1977; MATEUS 2006). As Sr isotope stratigraphy is limited to marine sediments, the Lourinhã formation could not be dated by this method.
In the south, the Lourinhã formation is interfingering with a succession of rather heterogeneous marginal-marine, brackish and limnic-fluvial strata, the **Farta Pao formation**, which originally (*sensu* LEINFELDER & WILSON 1989; LEINFELDER 1993) comprised the former Pterocérien (CHOFFAT 1885, 1901) (= Arranhó formation of LEINFELDER 1993), and the overlying Freixial formation (cf. CHOFFAT 1901). Later, the Sobral formation, a unit established by LEINFELDER (1986), was considered a member of either the Farta Pao formation (LEINFELDER & WILSON 1998) or the Lourinhã formation (PENA DOS REIS et al. 1996;

LEINFELDER & WILSON 1998). Additionally, the coastal Praia Azul member of Santa Cruz, originally assigned to the Lourinhã formation (HILL 1989), was placed in the basal Arranhó formation by LEINFELDER (1993). In order to resolve this confusion, we proposed a single formation with four members, i.e. the Farta Pao formation, which is the oldest available name uniting all of these strata (SCHNEIDER et al. in press). Both the members and formation still require formal establishment. Based on microfossils the Farta Pao formation as a whole ranges from the latest Early Kimmeridgian to the end of the Tithonian (cf. RAMALHO 1971a, LEINFELDER 1986). The Sr isotope data, however, indicate a significantly younger, late Late Kimmeridgian age for the base of the formation, which agrees well with the data from the underlying Amaral Formation.

The **Sobral member**, largely composed of brackish water deltaic sandstones, stretches from south of Arruda dos Vinhos westwards to the Atlantic and reaches northward along the coast up to Praia do Areia Branca west of Lourinhã, where it is directly overlain by the Lourinhã formation (MANUPELLA 1998). Most age specifications in the literature are based on LEINFELDER's (1986) initial interpretation, in which the Sobral member was largely placed in the Late Kimmeridgian (e.g. MANUPELLA et al. 1999; SCHMID & WERNER 2005; YAGÜE et al. 2006). However, Sr isotope data indicate a latest Late Kimmeridgian to middle Early Tithonian age (SCHNEIDER et al. in press), which is significantly younger than the Late Kimmeridgian age proposed by LEINFELDER & WILSON (1998).

The **Arranhó I member**, primarily found on the high grounds between Arruda dos Vinhos and Bucelas, comprises nodular micritic limestones characterised by the abundant large bivalves *Arcomytilus morrisii* and *Protocardia gigantea*. The latter species is confined to this member. At Santa Cruz, this unit forms a thin carbonate interval that is also characterised by *Protocardia gigantea*. Based on Sr isotope ages, this carbonate incursion reflects a supra-regional event at the Kimmeridgian-Tithonian boundary (SCHNEIDER et al. in press, accepted). As a cause for this phenomenon, LEINFELDER (1986) suggested a temporal stop of hinterland sedimentation. However, Sr isotope data indicate that the sediments of Sobral, Arranhó I, and Arranhó II members partially were deposited simultaneously, and thus contradict LEINFELDER's (1986) hypothesis. Apparently, a common succession of Sobral, Arranhó I, and Arranhó II members, as suggested by LEINFELDER & WILSON (1998) does not exist.

The **Arranhó II member** is a heterogeneous succession of marginal-marine to limnic-fluvial siliciclastics and marls, deposited in environments of pending salinities, similar to the Alcobaça formation. Locally, coral reefs and associated shallow-water carbonates may occur. The occurrence of the bivalve *Myophorella lusitanica* is clearly limited to this member. North of Bucelas, these strata are widely distributed. They also form large parts of the coastal sections at Santa Cruz and south of the Rio Sizandro. Sr isotope values suggest a late Late Kimmeridgian to late Early Tithonian age (SCHNEIDER et al. in press), which matches data inferred from microfossils (FÜRSICH 1981c; FÜRSICH & WERNER 1986; LEINFELDER 1986) and seismic mapping (RASMUSSEN et al. 1998), but not fully with sequence stratigraphy, which indicates an Early Tithonian age for the entire Arranhó (LEINFELDER 1993; LEINFELDER & WILSON 1998).

The youngest Jurassic lithostratigraphic unit of the area, the **Freixial Member**, is restricted to the southern parts of the Arruda and the eastern Turcifal subbasins. It is largely composed of limestones and sandy limestones with increasing intercalations of marine and terrestrial sandstones towards the top. The lithostratigraphic term and type locality at the village Freixial were established by CHOFFAT (1887) (RAMALHO 1971a; LEINFELDER 1986). Although restricted to certain facies, the bivalve *Buchotrigonia freixialensis* and the foraminifer *Anchispirocyclina lusitanica* may serve as index fossils for the Freixial Member. The Late Tithonian age inferred from Sr isotope values (SCHNEIDER et al. in press) corresponds well to microfossil data (REY et al. 1968; RAMALHO & REY 1969, 1975; RAMALHO 1971a, 1981; LEINFELDER 1986).

4. Fossil flora and fauna

Studying a particular group of fossils, it is always worth looking at the co-occurring flora and fauna in order to gain additional information on habitats and palaeoenvironment. Several Upper Jurassic strata of the Lusitanian Basin yield an exceptionally rich, diverse and often well-preserved fossil fauna. In particular, some of these sediments are famous for their **dinosaurs** and dinosaur trackways (e.g. LAPPARENT & ZBYSZEWSKI 1957; DANTAS 1990; DE RICQLES et al. 2001; ANTUNES & MATEUS 2003; BARDET et al. 2006; MATEUS 2006; ESCASO et al. 2007; SUNER et al. 2008). Moreover, scientifically important assemblages of early **mammal remains** have been discovered mainly but not exclusively from the locality of Guimarota (e.g. KÜHNE 1961; HAHN 1969; HENKEL & KRUSAT 1980; LILLEGRAVEN & KRUSAT 1991; HAHN & HAHN 1999, 2001; MARTIN 2002). Other vertebrates described from the respective strata include **fish** (KRIWET 1997, 1998, 2002, 2004; BALBINO 2003), **crocodiles** (KREBS 1967, 1968; BUSCALIONI et al 1996; SCHWARZ 2002; SCHWARZ & FECHNER 2004; SCHWARZ & SALISBURY 2005), **lizards** (SEIFFERT 1973), **turtles** (BRAEM 1973; ANTUNES et al. 1988; KOHRING 1990, 1998; PEREZ GARCIA et al. 2008), and **?birds** (WEIGERT 1995). An overview on the fossils from the Guimarota ecosystem can be found in KÜHNE (1968) and MARTIN & KREBS (2000). Fish otoliths and selachian teeth have also been found in several of our samples from the Arranhó II member and the Lourinha formation and are currently under study.

The Late Jurassic flora of the Lusitanian Basin is represented by **macroscopic plant remains** (TEIXIERA 1948, 1950; PAIS 1974, 1998; BRAUCKMANN 1978; WRIGHT & AZEREDO

2006), **charophyceans** (GRAMBAST-FESSARD & RAMALHO 1985; SCHUDACK 1993; PEREIRA et al. 2003), **calcareous algae** (RAMALHO 1968, 1971a, b; LEINFELDER & WERNER 1993), and **pollen and spores** (RILEY 1974; VAN ERVE & MOHR 1988; MOHR & SCHMIDT 1988; MOHR 1989; CASTRO 1996; SOUSA 1998; BARRÓN & AZEREDO 2003). However, no sound palynostratigraphic concept is available for the basin.

Nanofossils were studied by DE KAENEL et al. (1996). Invertebrate microfossils mainly encompass **foraminifera** (RAMALHO 1969, 1971a, 1990; RAMALHO & REY 1969; BERNIER et al. 1979; STAM 1986; WILLIAMSON & STAM 1988; AGTERBERG et al. 1990) and **ostracoda** (HELMDACH 1971a, b, 1972, 1974, 1991; HELMDACH & RAMALHO 1976; CABRAL & COLIN 1992; COLIN et al. 2000; CABRAL et al. 2001), which, however, are only rarely of stratigraphical value.

Sponges are represented by all groups that produce rigid mineral skeletons, i.e. Calcarea (FÜRSICH & WERNER 1991), Hexactinellida (TERMIER et al. 1985a, b; LEINFELDER et al. 1993), and coralline sponges (FÜRSICH & WERNER 1991; WERNER et al. 1994; SCHMID & WERNER 2005). In a single level of the Alcobaça formation, sponges represent a major constituent of the *Comophyllia polymorpha-Crispispongia* cf. *expansa* association that occurs at various localities of the Bombarral Subbasin (FÜRSICH & WERNER 1991).

A remarkably rich and diverse fauna of **scleractinian corals** characterises several fully marine environments, namely from the Alcobaça, Abadia, and Farta Pao formations (KOBY 1904-1905; GEYER 1955; OSCHMANN 1989). For example, 64 taxa have been listed from a single horizon of the Alcobaça formation (FÜRSICH & WERNER 1991). Moreover, corals have formed reefs in elevated marginal positions surrounding the subbasins (ELLIS & WILSON 1987; ELLIS et al. 1990; LEINFELDER 1992, 1993). In the CLB, coral reefs dominate the facies architecture of large parts of the Amaral Formation (NOSE & LEINFELDER 1992, 1997; NOSE 1999). A peculiarity of the Lusitanian Basin are reefs of the Arranhó II member, built almost exclusively by the coral *Amphiastrea piriformis*, which was obviously tolerant to reduced salinity (LEINFELDER & WERNER 2004; FÜRSICH et al. submitted).

As already noted, **bivalves** are the most common and possibly also most diverse invertebrates in the studied strata. More than 160 species in 44 families have been recorded (Table 1). However, only a few of these taxa are abundant in several strata and over a long time span. Daniel SHARPE was the first scholar to describe and figure several bivalve taxa in the course of geological investigations in the CLB (SHARPE 1850). A first monographic account of the Jurassic bivalves was conducted by Paul CHOFFAT (1885-1888, 1893a). After a long phase of cessation, bivalve research was revived in the 1980s, aiming on the taxonomy, palaeoecology and taphonomy of these organisms (FÜRSICH & SCHMIDT-KITTLER 1980; FÜRSICH 1981b, c; FÜRSICH & WERNER 1984, 1985, 1986, 1988, 1989a, b, 1991; FRENEIX & QUESNE 1985; WERNER 1986; YIN et al. 1995; SCHNEIDER & WERNER 2007).

However, several bivalve groups, i.e. oysters, palaeoheterodonts and heterodonts, have not yet been treated systematically. Moreover, certain outcrop areas especially of Oxfordian strata, e.g. the slopes of the Cesareda plateau or the Serra dos Candeiros, have not been sampled by CHOFFAT or for the present studies, but a few bivalve taxa are reported in the literature exclusively from these areas. Consequently, the list of Upper Jurassic bivalves from the Lusitanian Basin (Table 2) contains several taxa in open nomenclature.

In comparison to bivalves, **gastropods** occur much less frequent and diverse. However, certain levels in the Cabo Mondego, Alcobaça and Farta Pao formations are characterised by mass occurrences of ?*Pseudomelania* or nerineids. Large *Amauropsis* s. lat. and the neritid *Fuersichella bicornis* are common elements of the *Eomiodon securiformis*/nerineid sp. B association of the Alcobaça and Farta Pao formations (SCHNEIDER & WERNER 2007; SCHNEIDER et al. submitted). Additionally, small Cerithioidea (cf. *Cryptaulax*; cf. *Andangularia*) occur in abundance in soft bottom faunas of the Arranhó II member. A number of gastropod taxa have been mentioned in faunal lists or as constituents of certain assemblages (WERNER 1986; FÜRSICH & WERNER 1986, 1991), but only few species have been formally described (SHARPE 1850; BANDEL 1991).

With few exceptions, **cephalopods** are absent from the studied strata, while they are relatively common in limestones of the Cabaços and Montejunto formations mainly in the Arruda Subbasin. Several ammonites and belemnites have also been documented from the Alcobaça and Abadia formations. A single nautilid was found by the author in a bed of the Arranhó II member at Santa Cruz. A first description of the Upper Jurassic ammonite fauna was given by CHOFFAT (1893b). Later these fossils were in part re-examined mostly with regard to biostratigraphy (RUGET-PERROT 1961; ATROPS & MARQUES 1986; 1988a, b, c; MARQUES et al. 1992, 1996).

Not more than a handful of **bryozoan taxa** have been figured or listed from the studied strata (WERNER 1986; FÜRSICH & WERNER 1991), but still await systematic description.

The **brachiopod fauna** of the Jurassic of Portugal has been initially described by CHOFFAT (1947). However, he recorded only a few taxa from Upper Jurassic strata. Several rhynchonellides and thecideidinides from fully marine assemblages of the Alcobaça (FÜRSICH & WERNER 1991) and Abadia formations (personal observation) have never been described.

Crustaceans have mainly been recorded by indirect evidence, i.e. by their traces, now preserved as ichnofossils (FÜRSICH 1981a; SCHWEIGERT et al. 1997; NETO DE CARVALHO & RODRIGUEZ 2007).

Serpulid tubes have been found in several strata encrusting skeletal hard parts such as bivalve shells, corals and sponges (FÜRSICH & WERNER 1991; FÜRSICH et al. submitted), but were never described in detail.

A first comprehensive study on the **echinoderms** was conducted by the French invertebrate specialist Paul DE LORIOL (1890). This monograph, however, was followed only by a few short descriptions of individual taxa (FÜRSICH & WERNER 1991; WILLE 2002; SCHNEIDER & WERNER 2007). The most common echinoderm representatives are cidarid echinoids of the genus *Pseudocidaris*. Their club-shaped spines occur in great abundance in several strata and partially preserve their initial colour pattern (SCHNEIDER & WERNER 2007). Crinoids form an important part of the *Comophyllia polymorpha-Crispispongia* cf. *expansa* association found in the Alcobaça formation, and occur as frame builders in the crinoid-coral-algal build-ups of the Serra Isabel level in the uppermost Abadia Formation. Occasionally, starfish ossicles are found in sieve samples of several strata. Moreover, ophiuroid skeletal elements occur in abundance in several samples mainly from the Amaral and Farta Pao formations, and are currently subject of scientific studies.

At first glance, the compilation of flora and fauna given above describes a picture of side by side flourishing marine and terrestrial biota. This is surely true, but there is something in between: A large portion of the Upper Jurassic sediments deposited in the Lusitanian Basin formed in shallow-water lagoonal habitats under more or less brackish conditions and are therefore characterised by relatively low diverse faunal associations composed of species tolerant or even prone to these conditions. Most of the target taxa of the present study are part of these communities (SCHNEIDER et al. accepted, submitted).

LÉON PAUL CHOFFAT (1849-1919)

Historical perspective: The work of LÉON PAUL CHOFFAT

The history of scientific exploration of the Mesozoic strata of Portugal could not be thought without the work of Léon Paul CHOFFAT. After an initial geological study on parts of the southern CLB by Daniel SHARPE (1850), CHOFFAT was the one who set the standards in geology and stratigraphy of the Jurassic and Cretaceous rock succession in the Lusitanian Basin and introduced most of the lithostratigraphic units and terms still used today (e.g., CHOFFAT 1882, 1885, 1885-1900, 1887, 1901). Moreover, CHOFFAT was an excellent palaeontologist. He produced monographs on the ammonites (CHOFFAT 1893b, c), bivalves (CHOFFAT 1885-1888; 1893a) and brachiopods (CHOFFAT 1947) of the Jurassic of Portugal and on the Cretaceous invertebrate fauna of Portugal (CHOFFAT 1886-1902) and the former Portuguese colonies Angola (SW Africa; CHOFFAT & DE LORIOL 1888) and Moçambique (SE Africa; CHOFFAT 1903). In taxonomy, he was clearly ahead of the times as he often recognised the large morphological variability within a species and for the most part did not follow the widespread custom of over-splitting. His unique collection of fossils from Portugal represents one of the major parts of the present collections of the Muséo Geológico at Lisbon. His detailed, outstanding documentation and accurate labelling, gluing small, mostly printed paper labels including locality names and numbers of horizons corresponding to his field notebooks on every single specimen, can not be overvalued as a source of information today. Clearly, these samples, together with the publications that resulted from this material, form an important part of Portugal's scientific heritage.

Fig. 3. Examples from fieldwork in the Lusitanian Basin. A. Coastal section of the Alcobaça formation at Consolação. B. Gastropod shell bed mainly composed of ?*Pseudomelania* sp.; Cabo Mondego formation at Cabo Mondego. C. Building site section exposing a heterogeneous succession of sediments attributed to the Arranhó II member, Farta Pao formation, Serra de Alrota. Sample levels are indicated. D. Road cut section of the Sobral member, Farta Pao formation, east of Arranhó with *Eomiodon* sample level indicated by arrow. E. Ploughed field west of Serra de Alrota; Arranhó II member; sample spots of *Myophorella* are indicated. F. Sample of *Arcomytilus* and *Protocardia* collected in fields at Chão da Cruz, Arranhó I member, Farta Pao formation.

5. Material

The fossils for this study stem from the Monte Real, Bombarral, Arruda, Turcifal and Lower Tagus subbasins and from a number of localities along the Atlantic coast (Fig. 1). Most specimens were collected by Franz T. Fürsich, Winfried Werner and the author from rocks exposed in road-cuts, quarries and along the coastline or from weathered surfaces and ploughed fields, mainly during two field campaigns in 2005 and 2006. Additional material came from the CHOFFAT collection, deposited at the Muséo Geológico of the Instituto Geológico e Mineiro (IGM, Lisbon-Alfragide). Moreover, several species and specimens of bivalves from the collections of the Muséum National d'Histoire Naturelle at Paris were considered for comparison and included in part of the analyses.

With regard to lithostratigraphy, the Late Jurassic fossils from Portugal can be assigned to the Cabo Mondego, Cabaços, Alcobaça, Abadia and Farta Pao formations; the latter is divided into four members (Sobral, Arranhó I, Arranhó II and Freixial members), which are treated as separate units herein (Fig. 2).

Most of the figured specimens from Portugal are deposited in the Muséo Geológico of the IGM (Lisbon). Additional material is deposited in the BSPG (Munich).

6. Methods

6.1. Isotope analyses

Isotope analyses were performed on oyster shells of *Praeexogyra pustulosa*, *Actinostreon gregareum* (synonym: *A. solitarium*) and *Nanogyra nana* and belemnite rostra of *Hibolites* sp.. All fossils were cleaned with a brush and water and/or by immersion in hydrogen peroxide and cut into half using a diamond saw, and polished slices were produced. The remaining shell material was ground into sub-millimetre-sized fragments using an agate mortar and pestle, dry-sieved, and the best-preserved shell pieces were selected under a binocular microscope, briefly immersed in 0.5 N hydrochloric acid to remove traces of diagenetic calcite, washed in ultrapure water and dried.

To assess the state of preservation of the shells, the polished slices were examined by cathodoluminescence microscopy. Additionally, the absolute contents of Mn, Fe, Sr, and Mg in the shells were determined by flame AAS (Perkin-Elmer AAS 3300; LMU Munich, Department of Earth and Environmental Sciences). Oysters containing more than 250 ppm of manganese were excluded from isotope analyses.

For strontium isotope analysis aliquots of the samples were dissolved in 9N HNO_3. Sr was purified and accumulated by ion-chromatographic column separation using a Sr-specific crown-ether resin (Sr-Spec ®; method modified from HORWITZ et al. 1992 and PIN & BASSIN 1992), loaded on Birk's solution on single-band W filaments, and isotope ratios were measured in static mode on two thermal ionisation mass spectrometers (Thermo Finnigan

MAT 261) at the BSPG and the DEES Munich. Measured isotope values were normalized for mass fractionation using the naturally invariant value for $^{88}Sr/^{86}S$ of 8.37521 and the exponential fractionation law. Accuracy and precision of the measurements were controlled by analysing reference material $SrCO_3$ NIST SRM 987. For matching of the oyster and belemnite data with the SIS look-up table (HOWARTH & MCARTHUR 2003), $^{87}Sr/^{86}Sr$ ratios were adjusted to a NIST SRM 987 value of $^{87}Sr/^{86}Sr = 0.710248$.

For oxygen isotope measurements the samples were milled using an agate mortar and pestle and weighed. Isotope values were measured on a Delta plus Thermo Finnigan MAT mass spectrometer coupled with a GasBench II preparation device. Measured values are adjusted to solid reference standards NBS-18, NBS-19, and “Pfeil” internal lab standard. Palaeotemperatures were reconstructed using the equation of ANDERSON & ARTHUR (1983): $T\ [°C] = 16.0 - 4.14(\delta^{18}O_{carbonate} - \delta^{18}O_{water}) + 0.13(\delta^{18}O_{carbon} - \delta^{18}O_{water})^2$ and assuming ice free poles ($\delta^{18}O_{water} = -1.2‰$ PDB).

6.2. Palaeoecological analysis

Three main categories of data that are essential for the interpretation of morphological variability in bivalve shells were directly obtained from the fossiliferous horizons. In a first step, the **sedimentology** of the respective layers was evaluated. Usually, the rocks were classified according to the established schemes of DUNHAM (1962) for carbonates and EN ISO 14688-1 (2002) for siliciclastics, based on field observation. Additionally, thin-sections were prepared from well-cemented rocks and analysed by binocular microscopy.

Knowledge on **taphonomy** is indispensable for drawing correct conclusions on palaeoecology, genuine habitat, transport and depositional environment of the bivalve assemblages. Therefore, shell beds predominantly containing the target taxa were investigated in order to illustrate the mode of their formation, their palaeoecological and their sequence stratigraphic significance and to assess the role of time-averaging. Shell concentrations were studied in the field and multiple taphonomic signatures of the concentrations were recorded (FÜRSICH et al. accepted).

Additionally, data on co-occurring organisms from all horizons containing the target taxa were gathered, in order to obtain information on former **benthic communities**. However, the collections from Portugal usually are qualitative in nature and may depict α-diversity but not relative abundance of the taxa. Supplementary to macrofossil collection, argillaceous and muddy sediment samples were processed by immersion in diluted hydrogen peroxide, wet-sieved down to a mesh size of 0.01 mm, dried and picked for microfauna, which was briefly investigated. Additionally, the thin sections were screened for fossils. Wherever possible, the fossil assemblages have been assigned to a community or association as defined by

FÜRSICH (1981a) and FÜRSICH & WERNER (1984, 1986, 1991). For a few samples new associations were defined (SCHNEIDER et al. submitted).

6.3. Morphometry

After chemical and/or mechanical preparation of bivalve shells, the length, height and partially thickness of all individuals were measured using a calliper (measuring accuracy: 0.5 mm). For incomplete specimens, dimensions were recorded at the latest entirely traceable growth line. Additionally, the length of the ligament area was recorded for *Isognomon*. As the completeness of the valves usually varies within a double-valved specimen, both valves were treated as independent individuals. Supplementary to the measurements, the numbers of radial (*Arcomytilus*, *Protocardia*) or commarginal ribs (*Trigonia*) and the number of resilifers in *Isognomon* were counted.

For outline analysis, the specimens were photographed with the plane of the latest entire growth stage horizontally aligned. Digital images were reduced to this growth stage using the rubber tool in Adobe® Photoshop CS. Subsequently, the contrast of the images was increased to obtain black and white images and the contours of the shell outlines were saved as x/y-coordinates using TpsDig 2.12 software (ROHLF 2008).

Fourier shape analysis is a well-established method for analysing outline shape based on a combination of sine and cosine waves (KUHL & GIARDINA 1982; CRAMPTON & HAINES 1996) that has been successfully applied to extant and fossil bivalves (CRAMPTON & MAXWELL 2000; HAINES & CRAMPTON 2000; PALMER et al. 2004; SCHOLZ 2003; CRAMPTON & GALE 2005, 2009; SCHOLZ & HARTMAN 2007a, b). From several available methods for this procedure FFT (Fast Fourier Transformation; programs Hangle, Hmatch and Hcurve designed by CRAMPTON & HAINES 1996) was chosen because of certain advantages discussed at length by HAINES & CRAMPTON (2000). The outlines were automatically smoothed, and the number of harmonics that sufficiently describe the shell shape was visually estimated by trial and error. Due to the lack of sharply defined homologous points along the outline, all data sets were normalised for starting positions using the program Hmatch. By reversion of the Fourier transformation, idealized synthetic outlines were generated running the program Hcurve.

6.4. Statistical analyses

Height/length ratios, size distribution and numbers of ribs were displayed in scatter plots and box plots. The significance of the latter was tested applying one-way ANOVA. The measurements are generally based on adult specimens that can be identified by the crowding of growth lines in mature individuals, but also include a minor portion of juvenile or sub-adult individuals, which account for negative outliers and may enlarge the extension of the lower ranges of the boxes.

The Fourier coefficients were analysed with regard to stratigraphic, palaeoecologic, taxonomic and ontogenetic aspects applying Principal Component Analysis (PCA) using SPSS 16.0 (SPSS Inc. 2007) and PAST 1.82b software packages (HAMMER et al. 2001). The number of relevant principal components was evaluated on their account of variance applying the broken stick model *sensu* JACKSON (1993). Plots of the first three principal components have been proven to best display the morphological variability of the species. Partially, 95 % confidence ellipses were plotted in order to avoid confusion by too many symbols in the plots. Additionally, series of artificial outlines were produced to illustrate the morphospace of the taxa. In order to detect ecophenotypic adaptations and evaluate their potential relationship to biogenic and non-biogenic factors, the data were grouped in populations. The term "population" is used herein for all specimens of a taxon derived from a single horizon. Most of these samples may not represent populations in a biological sense, but were subject to more or less distinct time-averaging (WALKER & BAMBACH 1971; FÜRSICH & ABERHAN 1990; KIDWELL & BOSENCE 1991).

7. Results and discussion

7.1. Isotope analyses

Of more than 90 samples, less than 10% were excluded from isotope measurements because of diagenetic alteration. More than 90 % of the remaining samples produced sound Sr isotope values that could be translated into numerical ages (SCHNEIDER et al. in press). The main results of Sr isotope stratigraphy are incorporated and discussed in the "Lithologic and stratigraphic overview" section above. For the Upper Jurassic of the Lusitanian Basin, Sr isotope stratigraphy based on oyster shells is regarded highly successful, because oyster shells from most strata were to a large degree diagenetically unaltered, and age calculations fit well in the lithostratigraphic context.

The recalculation of palaeotemperatures is affected by somewhat higher uncertainties. In shells from brackish-water environments freshwater mixing may have significantly influenced the original sea-water oxygen isotope composition (SHARP 2007). Consequently, only cases of two or more samples from the same, fully marine horizon yielding similar isotope values were considered for temperature reconstruction. The palaeotemperatures recalculated from the oyster samples suggest 16-22.5°C for the Late Oxfordian-Early Kimmeridgian and 15.5-19°C for the Late Kimmeridgian. Three belemnite samples from the Lower to Upper Kimmeridgian Abadia Formation yielded isotope values indicating 12-14°C (SCHNEIDER et al. submitted). These values are in good accordance with temperature predictions for the region derived from global circulation models (MOORE et al. 1992; VALDES & SELLWOOD 1992). Moreover, the offset in temperature between oyster and belemnite samples is within the typical range attributed to differences in life style of these organisms and thus confirms the validity of our data (e.g. ANDERSON et al 1994; WIERZBOWSKI & JOACHIMSKI 2007). As can be seen from the measurements, temperatures did not change significantly during the Late Oxfordian to latest Kimmerdigian and thus may not have influenced any changes in bivalve life in the basin (SCHNEIDER et al. submitted).

7.2. Shell concentrations

Upper Jurassic bivalve shell beds in the Lusitanian Basin occasionally occur in fully, but more commonly in marginal marine environments. Mainly due to high environmental stress in these habitats resulting from fluctuating salinities or constantly brackish or hypersaline conditions, these shell concentrations are often mono- to paucispecific and characterised by large-sized, brackish-water endemic or opportunistic species (e.g., FÜRSICH & WERNER 1986; SCHNEIDER et al. submitted). Because of their greater tolerance to environmental perturbations compared to other macrobenthic organisms, bivalves are the dominant faunal element in the Upper Jurassic of the Lusitanian Basin and with exception of a few lagoonal shell beds that are composed of nerineid or ?*Pseudomelania* gastropods (e.g. Cabo Espichel: FÜRSICH & SCHMIDT-KITTLER 1980; Cabo Mondego: Fig. 3B), all concentrations are dominated by bivalves (FÜRSICH et al. accepted). The absence of competitors and a high input of nutrients by freshwater runoff led to the establishment of large populations. Usually, salinity-controlled environments are only weakly connected to the open sea and thus characterised by low-energy conditions and minor reworking of the sea floor. As a result, concentrations accumulated in-situ by the growth of many consecutive populations during relatively short time intervals (10^2-10^3 years) of reduced sediment input. Due to their simple ecological structure and only few generations of bivalves involved, time-averaging had little effect on these concentrations, and thus they provide an excellent database for palaeoecological analysis. In contrast, accumulations in more open shelf settings took significantly longer (10^3-10^4 years), and shell beds were increasingly affected by in-situ reworking and time-averaging (FÜRSICH et al. accepted). Commonly, concentrations are composed of epibyssate or endobyssate taxa (*Isognomon*, *Juranomia*, *Rostroperna*, *Alaperna*) or small patch reefs of cementing forms (*Praeexogyra*, *Nanogyra*, *Actinostreon*, *Harpax*), but rarely also of infaunal bivalves (*Eomiodon*, *Myophorella*). As an exception, *Juranomia* concentrations are predominanty controlled by physical processes.

The accumulation of the bivalve concentrations was strongly controlled by the rhythm of depositional sequences. Most shell beds formed during maximum flooding, when sediment input was at a minimum. More rarely, concentrations accumulated during the advanced transgressive systems tract, when reworking of bottom sediments had largely ceased.

Based on the biofabric and the taphonomic signatures of shells the mode of formation of the bivalve concentrations can be reconstructed, their post-mortem distortion and thus their usefulness for palaeoecological analysis can be evaluated, and they can be utilized for palaeoenvironmental analysis. Most of the taxa discussed here also form concentrations in other shelf seas of the Boreal and Tethys realms during the Late Jurassic. In the Lusitanian Basin, however, these shell beds are more common than in other regions due to the presence of widespread marginal marine environments (FÜRSICH et al. accepted).

7.3. Benthic associations and assemblages

Most of the macrobenthic assemblages sampled for the present study can be assigned to the associations proposed by FÜRSICH (1981c) and FÜRSICH & WERNER (1984, 1986, 1991). The term *Isognomon rugosus* association is used both for associations containing *I. rugosus* or *I. lusitanicus* herein in order to provide palaeoecological comparability. A **new subset** of this association, recorded from bioclastic marls of the Sobral member has been proposed, that is almost exclusively composed of *Isognomon lusitanicus*, accompanied by two taxa of small gastropods, rare solitary corals and a relatively low diverse microfauna, and indicates euhaline or slightly brachyhaline salinities (SCHNEIDER et al. submitted).

Moreover, the ***Eomiodon securiformis*/nerineid sp. B association**, found in certain strata of the Alcobaça formation and Sobral member, has been newly defined. Typically, this association is dominated by *E. securiformis* and a relatively small, moderately high-coiled nerineid gastropod (nerineid sp. B of FÜRSICH & WERNER 1986). Additionally, large *Amauropsis* s. lat., *Fuersichella bicornis* and *Anisocardia* (*Antiquicyprina*) sp. B (*sensu* FÜRSICH & WERNER 1986) are common, and a variety of bivalve taxa and several corals may occur (SCHNEIDER et al. submitted).

Three new assemblages have also been noted. (1) The autochthonous ***Arcomytilus morrisii/Corbulomima suprajurensis* assemblage** from marly clay of the Arranhó II member is characterized by abundant *A. morrisii* clusters, a relatively low-diverse fauna of small endobenthic bivalves dominated by *Corbulomima suprajurensis* and a remarkably diverse echinoderm fauna. (2) The parautochthonous **chaetetid-terebratulid-*Arcomytilus* assemblage** from the Cabaços Formation is mainly composed of small globular chaetetid colonies, terebratulid brachiopods and disarticulated *Arcomytilus* shells. (3) The autochthonous ***Regulifer beirensis* assemblage** from the Cabaços Formation is dominated by *Regulifer beirensis*, with occasionally associated *Isognomon rugosus* and *Camptonectes auritus*. While assemblages (1) and (2) are clearly attributable to fully marine conditions, assemblage (3) may have lived in a slightly brachyhaline environment (SCHNEIDER et al. submitted).

7.4. Phylogeny and ecophenotypy of the target taxa

Bivalves of five genera, i.e. *Arcomytilus*, *Isognomon*, *Trigonia*, *Eomiodon*, and *Protocardia*, were analysed using morphometric techniques. In four of these genera and in several additional bivalve taxa an abrupt **size increase** occurred soon after the Early-Late Kimmeridgian transition. However, there are certain differences with regard to the exact timing and pattern of this process among genera. For example, the size increase in *Arcomytilus*, *Eomiodon* and *Coelastarte* took place within species. In *Isognomon*, this step occurred significantly earlier than in *Arcomytilus* and was coupled with the speciation of *I. lusitanicus* (SCHNEIDER et al. submitted). In several other genera, e.g., in *Myophorella*, *Jurassicorbula* or *Protocardia*, small species were replaced by significantly larger descendents. Whether *Protocardia intexta*, however, was the direct ancestor of *P. gigantea* seems doubtful. Moreover, *P. gigantea* appeared not until the latest Kimmeridgian, and the small *P. peraltaensis* stayed small throughout the Kimmeridgian and Early Tithonian (SCHNEIDER et al. accepted), suggesting a different mechanism that triggered growth in this genus. Nevertheless, a major part of the bivalves in the Lusitanian Basin underwent size increase, and an increased nutrient supply is proposed as the major force behind this process. From several extant Mytilidae we know that increased productivity leads to an increase in shell growth, and this may also apply to fossil bivalves in Portugal, all the more as other reasons can largely be excluded (SCHNEIDER et al. submitted).

Two of the analysed genera belong to the Pteriomorphia. The radially ribbed mytilid genus ***Arcomytilus***, presumably specimens of the widespread species *A. pectinatus*, entered the Lusitanian Basin soon after the initial Middle Oxfordian transgression. First representatives are found e.g., at Cabo Mondego and Cesareda. However, these specimens already show morphological characteristics of the Lusitanian species *Arcomytilus morrisii* (SHARPE, 1850). Obviously, this species gradually evolved from *A. pectinatus* during the Middle Oxfordian in the Lusitanian Basin. Subsequently, *A. morrisii* became one of the generalists among the Upper Jurassic fauna in Portugal up to the beginning of the Late Tithonian. It is frequently found as a member of several fully marine or brackish-water associations. Most commonly, however, it forms large clusters in micritic limestones or fine siliciclastics attributable to shallow brackish-water lagoonal settings. In carbonates, *A. morrisii* is often accompanied by *Protocardia gigantea*, rare other infaunal heterodonts and a few, usually small oysters growing on the shells of *Arcomytilus* (SCHNEIDER et al. accepted, submitted).
In *Arcomytilus*, Fourier shape analysis revealed no significant changes in outline with time. Variability was rather controlled by the type of sediment, and specimens from soupy substrates frequently display a triangular outline with strongly protruding umbones that extended deeply into the sediment during life, while slender individuals with a straight anterior margin were adapted to epifaunal settlement (SCHNEIDER et al. submitted). There is

an overall decrease in the numbers of ribs in *Arcomytilus morrisii* with time. However, populations from the Sobral member contradict this trend, and an enormous variation occurs between specimens within individual strata. As a result, neither rib number nor outline shape can be used to determine each single specimen of *Arcomytilus* to species level without doubt. Large sample sets are indispensable to assess specific variability and to define the typical shape and morphospace of a species. Nonetheless, there will always be specimens positioned near the margins of this morphospace that overlap with the morphospace(s) of (an)other species (SCHNEIDER et al. submitted). This is a common feature both in fossil and extant Mytilidae, which is well-illustrated by the detection of extant cryptic species identifiable only by molecular genetics (GOSLING 1992a, b; MAAS et al. 1999; LEE & Ó FOIGHIL 2004, 2005).

The type genus of the Isognomonidae, ***Isognomon*** s. str., characterised by a large number of more or less evenly spaced resilia and resilifers in an almost straight multivincular ligament, occurs with four species in the Upper Jurassic of the Lusitanian Basin. Two of these lived epibyssate and are restricted to only few localities and comparably short time intervals in the area. Two other forms, *I. rugosus* and *I. lusitanicus*, are among the most common taxa in the Lusitanian Basin. *I. rugosus* obviously is a representative of the early colonisers, as it is relatively widespread in the Boreal Realm and appears in the lowermost beds of marine influence both in the Cabo Mondego and Cabaços formations. Characterised by a broad, flattened, heavy anterio-ventral shell portion and more or less pointed, tapering umbones, this species is adapted to an endobyssate, semi-infaunal life position, similar to *A. morrisii* (FÜRSICH 1980; SCHNEIDER et al. submitted). However, *I. rugosus* usually did not live in clusters, but rather formed densely populated patches or banks of sometimes remarkable extent (FÜRSICH et al. accepted).

The second species, *I. lusitanicus*, was regarded a junior synonym of *I. rugosus* by FÜRSICH & WERNER (1989b), but is now re-established based on morphometric analyses (SCHNEIDER et al. submitted). *I. lusitanicus* is a straight descendent of *I. rugosus*, which evolved in the Lusitanian Basin soon after the Early/Late Kimmeridgian transition. It is much larger than its ancestor and is characterised by a significantly lower number of resilifers per centimetre. Shell shape and life style are entirely similar to *I. rugosus*. However, larger shells may have increased intra-population competition for space resulting in an increase in intra-specific shape variability. Shells of *I. lusitanicus* are frequently found more or less in-situ and form thick autochthonous shell beds of several bivalve generations in outcrops along the Atlantic coast (FÜRSICH et al. accepted).

Both species display a great intra-specific variability in shell outline shape. However, Fourier shape analysis showed that most of this variability occurs within populations, while there are no significant differences between populations within single time slices or the stratigraphic column. In the Farta Pao formation certain shape types of *I. lusitanicus* are more abundant in certain subbasins, but from what we know about intra-population variability it seems unlikely that these forms represent subspecies *in statu nascendi* (SCHNEIDER et al. submitted).

The heterodont ***Eomiodon***, a representative of the Neomiodontidae, is a shallow burrowing suspension-feeder of veneroid shell shape. Representatives of this genus typically occur in brackish water habitats (HUCKRIEDE 1967; FRENEIX & CUBAYNES 1984; FÜRSICH & WERNER 1986). The specimens from the Lusitanian Basin are assigned to two species. A small, commarginally ribbed form is currently termed *Eomiodon* sp. A, as it cannot be assigned to a species with certainty without considering type material. The second, large species *Eomiodon securiformis* is common and widespread in different Upper Jurassic strata in the Lusitanian Basin at least since the Late Oxfordian, as it was found in abundance in several layers of the Cabo Mondego section. It often dominates associations or even forms monospecific shell beds (FÜRSICH et al. accepted) and displays a large variability in shell shape (SCHNEIDER et al. submitted). In contrast to *Arcomytilus* and *Isognomon*, however, variability in *Eomiodon securiformis* decreases with time, and specimens from the Farta Pao formation usually are short and high, with a blunt posterio-ventral shell portion. Several individuals from the Alcobaça formation retain commarginal lamellae in early growth stages that faint later in ontogeny. In large specimens from the Farta Pao formation, this peculiar early-growth-stage ornamentation may have been eroded due to burrowing movements. Despite of marked intra-population variability there are no significant differences in shape with time or between populations (SCHNEIDER et al. submitted). A single specimen of *E. securiformis* from the Kimmeridgian of the Algarve region (S Portugal) retained in the BSPG (Munich) shows that the species is not endemic to the Lusitanian Basin, but it has never been reported from outside Portugal.

Representatives of the shallow infaunal heterodont genus ***Protocardia*** predominantly occur as minor constituents in several more or less fully marine associations (WERNER 1986; FÜRSICH & WERNER 1986; SCHNEIDER et al. accepted). In Portugal, five species have been distinguished, two of which are of Tethyan and one of Boreal-Tethyan origin. Two other species are endemic to the Lusitanian Basin. Morphometric techniques, i.e. Fourier shape analysis, size measurements and counting of posterior radial riblets, enable a distinct separation of several species, but still afford the help of classical qualitative taxonomy in order to clearly distinguish all species (SCHNEIDER et al. accepted).

The scientifically most interesting representative of the genus is the newly described *Protocardia gigantea*, a literally gigantic species that reaches distinctly more than 10 cm in length, while most other “large” species of the genus range around 5 cm. In the CLB it can be used as a stratigraphic marker for the Kimmeridgian-Tithonian boundary, as it occurs exclusively in the Arranhó I member, which formed around that time. Large steinkerns of *P. gigantea* are common in particular horizons and can easily be identified in the field, which makes them diagnostic fossils for geologic mapping (SCHNEIDER et al. accepted).

During the Jurassic and Cretaceous, representatives of the family Trigoniidae form an important part of numerous shallow-marine benthic communities worldwide. The globally distributed Middle Triassic to Late Cretaceous genus ***Trigonia*** occurs in the Upper Jurassic of Portugal with a single species, named *Trigonia pseudomeriani* by CHOFFAT (1885-88). Shells of this species are found exclusively in fully marine levels of the Alcobaça formation, usually in marls and marly limestones containing a considerable fraction of small oncoids and bioclasts. The large variability of these shells, their close affinity to forms from the Oxfordian and Kimmeridgian of France and England, and the tremendous over-splitting of *Trigonia* in the literature prompted me to have a close look at this genus and develop a modern species concept for the specimens from Portugal. Based on this concept, which applies both morphometric techniques and classical taxonomy, these specimens are regarded as belonging to a descendant of *T. reticulata*, which is a variable, widespread and long-lived species, that occurs in the Lower Oxfordian-Upper Kimmeridgian of western and central Europe. *Trigonia pseudomeriani* is even more variable in shell shape than *T. reticulata*, but differs from its ancestor in a significantly higher density of flank costae and, even more important, a more distinctly angled posterio-dorsal shell margin (SCHNEIDER et al. in prep.). Moreover, it is endemic to the Lusitanian Basin and occurs only during a time span of less than 2 Ma at around the Oxfordian-Kimmeridgian transition.

In order to develop an idea about the origin, diversity and timing of diversification of *Trigonia*, more than 600 occurrences originally assigned to more than 150 species were evaluated based on literature data and plotted in global palaeogeographic maps. Species identification largely relies on literature data, and thus does not represent a systematic revision. Respectively, the palaeobiogeographic plots, which have already been completed for the Triassic and Jurassic, surely suffer from artefacts attributable either to over-splitting in well-explored regions (e.g. Western Europe) or understudy in areas that are difficult to access (e.g. central and Southeast Asia). Nevertheless, the maps do include a major part of the information available on diversity and dispersal of *Trigonia* (SCHNEIDER et al. in prep.).

To the current state, the species description in the Systematic Palaeontology section, the palaeogeographic map for the Cretaceous and the discussion on palaeobiogeography are lacking, and the manuscript may be regarded as 80% complete.

7.5. Colour pattern preservation

A peculiarity of the fossil record of the Upper Jurassic of the Lusitanian Basin is the preservation of colour patterns reported from five quite different organisms. The neritimorph gastropod *Fuersichella bicornis*, which, based on shell shape, was likely adapted to soft bottoms, shows a pattern of narrow colour bands that are more or less parallel to the direction of shell coiling. The intra-specific variability of this pattern is considerable (Schneider & Werner 2007). In neritimorphs, colour pattern preservation is a frequently occurring feature at least since the Silurian (Kríz & Lukes 1974), mostly attributed to melanin pigments, which are composed of protein complexes highly durable during any kind of diagenesis (Comfort 1950, 1951).

The semi-infaunal pterioidean bivalve *Isognomon rugosus* and the epibenthic reclining astartid *Coelastarte discus* both are vividly banded with patterns that do not coincide on the opposite valves. While *Isognomon* preserves colour that is subject to fading in the outer calcitic shell layer, the colour is intimately associated with radial shell parts in *Coelastarte*, suggesting different chemical composition of the pigments involved (Schneider & Werner 2007).

In the regular echinids *Pseudocidaris lusitanica* and *P. spinosa*, coloured blotches occur all over the club-shaped spines and are often arranged in radial bands. Preservation of colour patterns in echinids seems to be an extremely rare phenomenon (Schneider & Werner 2007) and a similarly vivid colouration or patterns comparable to those observed in *Pseudocidaris* have never been reported before. Among several unidentified pigments, certain quinones have been recorded to cause coloration in extant echinids (Anderson et al. 1969).

In most of these organisms, colouration may have been served as camouflage, since a pattern of blotches, spots or vivid stripes renders well-defined shapes and results in an optical break-up of outlines (Wicksten 1983). In *Isognomon*, however, this seems less probable because these bivalves commonly occur in dense colonies. In Portugal, colour pattern preservation occurs in several Upper Jurassic strata and localities. However, coloured and uncoloured specimens may occur within a single horizon, and thus no particular mechanism responsible for the preservation of pigmentation could be detected (Schneider & Werner 2007).

8. Conclusions

In the present study, bivalve shells from the Upper Jurassic of the Lusitanian Basin (central Portugal) have been analysed with a variety of techniques in order to gain data on a range of quite distinct subjects. Strontium isotope measurements on oyster shells produced sound results that enabled the establishment of a solid framework of numerical ages for the Upper

Jurassic of the Lusitanian Basin. Based on these values, the onset of sedimentation in the Middle Oxfordian is confirmed and a continuous sedimentary record up to the end of the Tithonian is proven. Moreover, chronostratigraphic correlation of diachronous strata is provided for several regions within the Lusitanian Basin. Fairly constant shallow water palaeotemperatures of 16-22°C have been reconstructed from stable oxygen isotope data for the Late Oxfordian to Late Kimmeridgian.

Several brackish water endemic or opportunistic bivalve taxa formed more or less autochthonous shell concentrations in several strata, which are largely attributed to phases of low sedimentation, i.e. during maximum flooding or the transgressive systems tract, and provide excellent data for palaeoenvironmental studies.

The combination of simple size measurements, counts of ornamentation elements or multivincular ligament grooves and Fourier shape analysis of shell outlines have revealed rather different modes of adaptation and speciation in the five bivalve genera *Arcomytilus*, *Isognomon*, *Eomiodon*, *Protocardia* and *Trigonia*. Most taxa display a significant but not absolutely simultaneous size increase at around the Early to Late Kimmeridgian transition, which occurs either within species or in larger descendents within genera. Since other reasons can widely be excluded, size increase is attributed to increased nutrient supply from river discharge. In *Arcomytilus morrisii*, shell shape varies with lifestyle, i.e. epibyssate versus semi-infaunal-endobyssate, and thus with sediment type, i.e. hard- or stabilised bottom versus soupy substrate. The number of radial ribs generally decreases with time, but exceptions occur relatively abundant. In *Isognomon*, size increase parallels speciation of *I. lusitanicus* which differs not only in size but in a significantly lower resilifer density from its direct ancestor *I. rugosus*. Shell outline variability is greater within than between populations, and no significant distribution pattern of shape types is evident. A remarkable variability with regard to outline shape is also seen within populations of *Eomiodon securiformis*. With time and size, however, overall variability decreases. In *Protocardia*, size increase may have a different background, as it occurs very late and a small representative of the genus still persists. The newly described species *Protocardia gigantea*, however, proves to be diagnostic for the Kimmeridgian-Tithonian boundary and can be used as a marker for geological mapping. Generally, species in *Protocardia* can partially be identified by morphometric techniques, but the aid of classical qualitative taxonomy is still needed. The same is true for *Trigonia*, which, however, may display considerable intraspecific variability with regard to shell shape and ornamentation and therefore was subject to enormous over-splitting in literature. For *T. reticulata* and its descendant *T. pseudomeriani*, a comprehensive modern species concept provides an impression of this variability, and may be further extrapolated to other species.

A peculiarity of the Upper Jurassic sediments in the Lusitanian Basin is the preservation of colour patterns in different fossil groups, i.e. bivalves, gastropods and echinids. Vividly coloured blotches, as described from the large spines of *Pseudocidaris*, have never been recorded before. In most of these organisms, colour patterns may have acted as a kind of camouflage.

Altogether, the analyses applied in these studies have helped to extract a significant amount of new information on bivalves and bivalve life in the Upper Jurassic of the Lusitanian Basin, but as anybody having seen these highly fossiliferous rocks will agree, there is still plenty of work ahead.

9. Future perspectives

9.1. Upper Jurassic bivalves from Portugal

Several species of the family Trigoniidae tentatively assigned to the genera *Buchotrigonia* and *Myophorella* occur in the Upper Jurassic of Portugal. Despite of a number of attempts by different scholars, the taxonomy and systematics of these genera is still far from settled, as it is to a large degree based on the ornamentation of the shell flank. However, the presence of knobs, ridges or ribs seems to be an easily modifyable character of minor phyletic significance that mostly depends on sediment type and grain size. This observation is underlined by the presence of a commarginally ribbed juvenile shell stage in all representatives of the mentioned genera and several other closely related taxa. Moreover, the ornamentation pattern, usually starting with regularly arranged ribs or rows of knobs, becomes increasingly irregular and often chaotic with growth and increasing inflation of the shells (Fig. 4). Presumably, these modifications serve to construct a consistently dense ornamentation on the whole shell surface (compare STANLEY 1977), which cannot be achieved by maintaining the regular ornamentation pattern. Interestingly, the two valves of a specimen are never identically ornamented, and an enormous variability in ornamentation may occur within populations. Moreover, there are strong differences between populations of a single species with regard to pattern and strength of ornamentation. The samples from Portugal consist of several hundred specimens from different localities and strata and therefore enable a comprehensive study on intraspecific variability. Additionally, large samples of an extremely variable population of *Myophorella bronni* from the Kimmeridgian Sables de Glos in NW France will be incorporated in this project. Because similar representatives of the family Trigoniidae form an important part of numerous shallow marine benthic communities all over the world, the results of these studies surely will be of global significance.

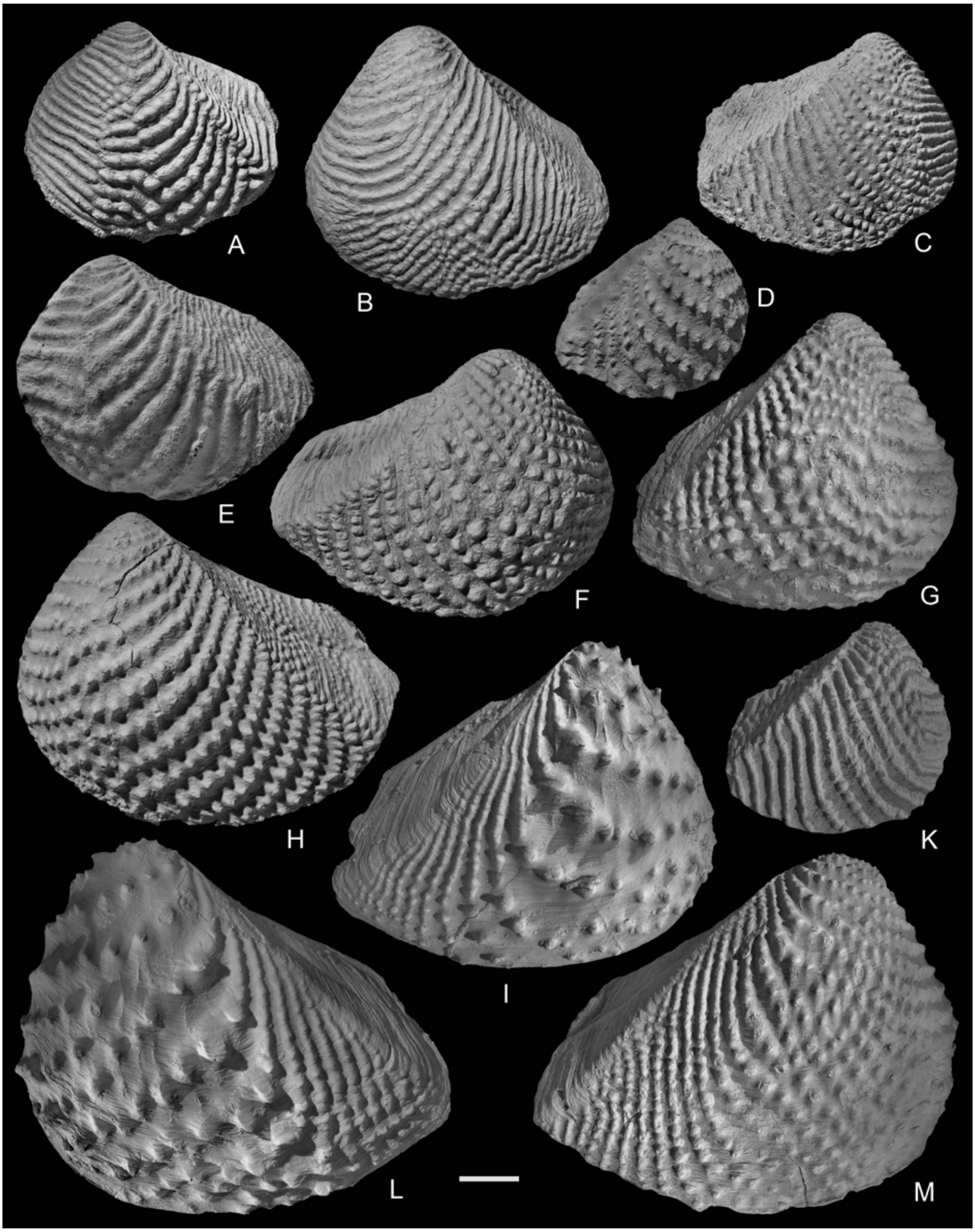

Fig. 4. A selection of *Myophorella* specimens from the Upper Jurassic of the Lusitanian Basin. A. ‘*Trigonia ribeiroi*’ CHOFFAT, holotype, Upper Jurassic, Cesareda. B. ‘*Trigonia alcobacensis*’ CHOFFAT, holotype, Alcobaça formation, near Alcobaça. C. Specimen of *alcobacensis*-type, Alcobaça formation, Chiqueda. D. Specimen of *muricata*-type, Alcobaça formation, Vestiaria. E. ‘*Trigonia juntoensis*’, nomen nudum. F. ‘*Trigonia neumayri*’ CHOFFAT, holotype, Alcobaça formation, Sobral da Lagoa. G. *Myophorella lusitanica* SHARPE, Arranhó

II member, S of Rio Sizandro. H. ‘*Trigonia muricata*’ GOLDFUSS, Alcobaça formation, near Alcobaça. I. *Myophorella lusitanica* SHARPE, Arranhó II member, Santa Cruz. K. Specimen of *alcobacensis*-type, Alcobaça formation, Barrio. L. *Myophorella lusitanica* SHARPE, Arranhó II member, Lameiro das Antas. M. *Myophorella lusitanica* SHARPE, Arranhó II member, Nossa Senora de Ajuda.

9.2. Transfer of concepts

The morphospace concepts developed in the present study can be transferred to other bivalve groups and other time slices. For example, the sister group of the Trigonioida, the Unionoida, displays an even higher variability with regard to shell shape and partially also ornamentation than the trigoniids. However, shell characters are known to be highly dependent on water chemistry and energy. Moreover, unionids were subject to a number of regional radiations in the ?Mesozoic and Cenozoic, usually bound to large river systems. Southeast Asia currently harbours more than 90 nominal species of extant Unionidae, which, however, remain poorly understood (GRAF & CUMMINGS 2007). Several genera (e.g. *Lamprotula*, *Cuneopsis*) show a remarkable diversity, which is presumably also a consequence of considerable over-splitting. Vice versa, hidden diversity is likely to occur. Clearly, the mentioned taxa are in need of modern species concepts, which can be achieved by applying the methods presented here, additional morphometric techniques (e.g. landmark analysis) and molecular genetics. Subsequently, these concepts can be adapted to fossil representatives of the respective genera, which were collected from Oligocene deposits in Vietnam during spring 2009 (BÖHME et al. submitted) in order to infer the phylogeny of Unionidae in relation to Cenozoic tectonics and flow regimes in Southeast Asia. Moreover, results on extant unionid diversity may play a role in future bioheritage concepts in Southeast Asia, as mussels are know to be highly sensitive of ecologic disturbance or pollution and may serve as ecologic indicators in this biodiversity hot spot.

Acknowledgements

The present work was financially supported by the German Science Foundation (DFG; project numbers Fu 131/31 and We 1152/2). I want to express my sincere thanks to the ladies of the Generaldirektion der Staatlichen Naturwissenschaftlichen Sammlungen Bayerns (Munich) for their excellent cooperation regarding all administrative purposes.

During my stays at Portugal Miguel M. Ramalho (Lisbon) enabled fieldwork and access to the museum collections. Octávio Mateus (Lourinha) stored my samples and provided information on geology. Rural people in Portugal were always friendly and helpful and it was a great pleasure to work on their land.

You may have different opinions on stones. You can love them or hate them, but in the end, you should be able to take it with a smile.

Didier Merle and Herve Senut kindly provided access to the collections and facilities of the Muséum National d'Histoire Naturelle at Paris.

Indispensable support came from the technical staff of the Bayerische Staatssammlung für Paläontologie und Geologie and the Department of Earth and Environmental Sciences of the Ludwig-Maximilians-University, Munich. The extensive and thorough preparation work of my student assistant Franziska Maier and the preparators Ulrich Projahn and Stefan Sonyi saved a lot of time. The perfect production of thin-slides by Cathleen Helbig was also a great support. Karin Paschert kindly provided the AAS analyses. Rene Neumaier and Andreas Hammer always provided immediate help in case of IT problems. My student assistant Tini Böhmer greatly aided with preparation of image files. Not to forget the excellent photographs produced by Georg Janßen (now Nürnberg).

My sincere thanks go to the isotope specialists for providing facilities, literature, and isotope measurements, and for giving useful advice: Ernst Hegner, Stefan Hölzl (both Munich), Michael Joachimski (Erlangen), Christoph Mayr, Alexander Rocholl, Susanne Rummel (all Munich) and Thomas Steuber (Abu Dhabi).

Several colleagues provided scientific support on various subjects: Alexander Altenbach (Munich), Gernot Arp (Göttingen), Andrew Francis, Anthony Hallam (both Birmingham), Reinhold Leinfelder (Berlin), Martin Nose, Alexander Nützel, Oliver Rauhut, Gerhard Schairer, Dieter Schmid (all Munich), Henning Scholz (Berlin). Thanks a lot to all of you for your help!

During almost eleven years here in Munich, many of the aforementioned persons and several others have not only been colleagues, but also have become good and reliable friends. Thanks a lot for your personal support, for interesting, serious and amusing conversations, for your company – and your patience!

Special thanks go to Jérôme Prieto (Munich) for his unconditional friendship and to Tanja Schulz-Mirbach (Munich) for her fine cooperation and continuous help in morphometrics, and for our inspiring and recreational “daily resume” after work.
Cheerioh to the „Glory Seven“, Judith Erl, Stefanie Klug, Thorsten Kowalke, Michael Krings, Ella Kunz, Helmut Mayr, and Ernst Rieber for their company, endless debates, generous help, and constructive criticism during all day and night, dry and wet seasons!
Four persons played a major role in making the present work a scientific success.
Michael Krings (Munich) taught me all the little things necessary to publish successfully, improved my English, and prompted me to look at my research from different directions during permanent discussions.
Michael Amler (Munich) acted as an assistant advisor without hesitation. Moreover, he understood this role not only as a duty, but also as a constructive participation.
Winnie Werner (Munich) was the one who had to stand my daily need for discussion and feedback. Without his permanent input of supplementary information on stratigraphy, ecology, literature, and taxonomy, the present work would surely be much more incomplete. Thanks a lot for always having an open ear, for investing an enormous amount of time, and for your patience.
Franz Fürsich (Erlangen) took it as a matter of course to act as my advisor when we started this project. Over the years of working he never put pressure on me, but was always present when I needed support. Gaining insight into his way of thinking and working, and benefiting from his know-how, was a great experience. Thanks a lot for believing in me and for the good times we had!
Finally, there are a number of persons who were, and still are, of great importance for the non-scientific part of my life. As this is an entirely personal issue, let me switch to German language now.
Mein besonderer Dank gilt:
Meiner besten Freundin Veronika Winkler-Stöhr.
Meiner Schwester Judith Schneider und Herbert Stark.
Meinem Vater Franz Schneider und Hannelore Friebel.
Auf sie alle konnte und kann ich mich immer und in jeder Beziehung verlassen.
Zu guter letzt möchte ich meiner Mutter Gerlinde Schneider danken, die, auch wenn sie mein Wirken und Werden nicht mehr erleben durfte, den Grundstein dafür gesetzt hat, meine Begabungen und Interessen zu entwickeln.

Family	**Species**
Nuculidae	*Palaeonucula inconstans* (Roeder, 1882)
	Palaeonucula menkii (Roemer, 1836)
	Lusitanula gomesi (Choffat; 1888)
Nuculanidae	*Mesosaccella sanctaecrucis* (Choffat, 1888)
	Nuculana (*Praesaccella*) *favrei* (Choffat, 1888)
	Nuculana (*Praesaccella*) *moeschi* (Choffat, 1888)
Arcidae	*Arca* (*Eonavicula*) *rutimeyeri* Loriol, 1892
	Arca (*Eonavicula*) aff. *trisulcata* Münster, 1837
	Grammatodon (*Grammatodon*) *concinnus* (Phillips, 1829)
	Grammatodon (*Grammatodon*) *hersilius* (d'Orbigny, 1850)
	Grammatodon (*Cosmetodon*) *elongatum* (J. de C. Sowerby, 1825)
	Cucullaea (*Idonearca*) *contracta* Phillips, 1829
	?*Cucullaria jurassica* Fürsich & Werner, 1988
	Isoarca texata (Münster, 1837)
	Isoarca cf. *explicata* Boehm, 1881
	Barbatia (*Barbatia*) *clythia* Loriol, 1892
	Trichites consolacionensis Choffat, 1888
	Trichites gemmelaroi Choffat, 1888
	Trichites lusitanicus Choffat, 1888
	Trichites sp.
Mytilidae	*Arcomytilus furcatus* (Münster, 1837)
	Arcomytilus morrisii (Sharpe, 1850)
	Arcomytilus sp.
	Regulifer alrotae Fürsich & Werner, 1988
	Regulifer beirensis (Sharpe, 1850)
	Inoperna perplicata (Etallon, 1863)
	?*Praemytilus* sp.
	Mytilus sp.
	Modiolus (*Modiolus*) *imbricatus* J. Sowerby, 1818
	Modiolus virgulinus (Etallon, 1863)
	Modiolus sp.
	Lithophaga (*Lithophaga*) *subcylindrica* (Buvignier, 1852)
	Lithophaga (*Lithophaga*) sp.
	Lycettia poikilohalina Fürsich & Werner, 1985
Pteriidae	*Pteria credneriana* (Loriol, 1866)
	Pteria gesneri (Contejean ex Thurmann, 1860)
	Pteria pygmaea (Dunker, 1837)
	Pteria rhomboidalis (Cornuel, 1841)
	Pteria cf. *plana* (Morris & Lycett, 1853)
Inoceramidae	*Parainoceramus* sp.
Isognomonidae	*Isognomon* (*Isognomon*) *lusitanicus* (Sharpe, 1850)
	Isognomon (*Isognomon*) *promytiloides* (Arkell, 1933)
	Isognomon (*Isognomon*) *rectangularis* Fürsich & Werner, 1989
	Isognomon (*Isognomon*) *rugosus* (Münster, 1835)
	Isognomon (*Rostroperna*) *thurmanni* (Contejean, 1860)

Family	**Species**
Pulvinitidae	*Pulvinites abadiensis* FÜRSICH & WERNER, 1989
Bakevelliidae	*Aguileria espichelensis* FÜRSICH & WERNER, 1989
	Alaperna polita (SHARPE, 1850)
	Bakevellia (*Bakevellia*) *parva* FÜRSICH & WERNER, 1989
	Costigervillia CHOFFATi FÜRSICH & WERNER, 1989
	Gervillia (*Gervillella*) *aviculoides* (J. SOWERBY, 1814)
	Gervillia (*Virgellia*) *sobralensis* SHARPE, 1850
	Gervillia cf. (*Gervillella*) *siliqua* (J. A. EUDES-DESLONGCHAMPS, 1824)
Palaeolophidae	*Rastellum* sp.
	Actinostreon gregareum (J. SOWERBY, 1818)
Gryphaeidae	*Nanogyra nana* (J. SOWERBY, 1822)
Ostreidae	*Praeexogyra pustulosa* (SHARPE, 1850)
	Liostrea moreana (BUVIGNIER, 1852)
Ostreoidea	Ostreoidea indet.
Pinnidae	*Pinna* cf. *radiata* MÜNSTER, 1837
	Stegoconcha occidentalis (CHOFFAT, 1888)
Limidae	*Plagiostoma laeviusculum* J. SOWERBY, 1822
	Pseudolimea duplicata (J. DE C. SOWERBY,1827)
	Antiquilima (*Ctenolima*) *aequilatera* (BUVIGNIER, 1852)
Posidoniidae	*Aulacomyella abadiensis* (FRENEIX & QUESNE, 1985)
	Bositra (?) *henrici* FÜRSICH & WERNER, 1989
Pectinidae	*Camptonectes* (*Camptonectes*) *auritus* (SCHLOTHEIM, 1813)
	Camptonectes (*Camptochlamys*) *clathratus* (ROEMER, 1836)
	Camptonectes (*Camptochlamys*) *obscurus* (J. SOWERBY,1818)
	Spondylopecten (*Plesiopecten*) *subspinosus* (SCHLOTHEIM, 1820)
	Spondylopecten (*Spondylopecten*) *palinurus* (D'ORBIGNY, 1850)
	Spondylopecten (*Spondylopecten*) *subpunctatus* (MÜNSTER, 1833)
	Radulopecten fibrosus (J. SOWERBY, 1816)
	Radulopecten scarburgensis (YOUNG & BIRD, 1822)
	Radulopecten sigmaringensis (ROLLIER, 1915)
	Radulopecten strictus (MÜNSTER; 1833)
	Eopecten obliquus FÜRSICH & WERNER, 1989
	Eopecten velatus (GOLDFUSS, 1833)
	Eopecten cf. *spondyloides* (ROEMER, 1836)
	Chlamys (*Chlamys*) *textoria* (SCHLOTHEIM, 1820)
Entoliidae	*Entolium* (*Entolium*) *corneolum* (YOUNG & BIRD, 1828)
	Entolium (*Entolium*) ?*zitteli* (GEMMELARO & DI BLASI, 1874)
Propeamussiidae	*Propeamussium* (*Propeamussium*) *nonarium* (QUENSTEDT, 1857)
Plicatulidae	*Plicatula* (*Plicatula*) *ogerieni* LORIOL, 1904
	Plicatula armata (GOLDFUSS, 1835)
	Atreta unguis (LORIOL ex MERIAN, 1900)
Terquemiidae	*Terquemia irregularis* (ETALLON, 1863)
Anomiidae	*Juranomia calcibyssata* FÜRSICH & WERNER, 1989
	?anomiacean bivalve

Family	**Species**
Trigoniidae	*Scaphotrigonia lorioli* (CHOFFAT, 1885)
	Buchotrigonia freixialensis (CHOFFAT, 1885)
	Buchotrigonia kobyi (CHOFFAT, 1885)
	Myophorella alcobacensis (CHOFFAT, 1885)
	Myophorella beirensis (CHOFFAT, 1885)
	Myophorella lusitanica (SHARPE, 1850)
	Myophorella muricata (CHOFFAT, 1885)
	Myophorella neumayri (CHOFFAT, 1885)
	Myophorella ribeiroi (CHOFFAT, 1885)
	Trigonia reticulata AGASSIZ, 1840
Unionidae	*Unio alcobacensis* CHOFFAT, 1885
	Unio buarcosensis CHOFFAT, 1885
	Unio danischi HUCKRIEDE, 1967
	Unio delgadoi CHOFFAT, 1885
	Unio heberti CHOFFAT, 1885
	Unio heimi CHOFFAT, 1885
	Unio mayeri CHOFFAT, 1885
	Unio veziani CHOFFAT, 1885
Astartidae	*Coelastarte discus* (SHARPE, 1850)
	Nicaniella (*Trautscholdia*) *supracorallina* (D'ORBIGNY, 1850)
	Nicaniella cingulata (CONTEJEAN, 1859)
	Nicaniella mysis (D'ORBIGNY, 1850)
	Nicaniella sp. A
	Nicaniella sp. B
	Nicaniella sp. C
	Prorokia cf. *kobyi* (GREPPIN, 1893)
Pholadomyidae	*Pholadomya* (*Bucardiomya*) *protei* (BRONGNIART, 1821)
	Pholadomya constricta (AGASSIZ, 1842)
	Pholadomya delgadoi CHOFFAT, 1885
	Homomya hortulana AGASSIZ, 1842
	Machomya jurensis (DUNKER, 1847)
	Pachymya (*Arcomya*) *castroi* (CHOFFAT, 1893)
	Pachymya (*Arcomya*) *cortazari* (CHOFFAT, 1893)
	?*Pachymya* (*Arcomya*) sp.
Ceratomyidae	*Ceratomya excentrica* (ROEMER, 1836)
Myopholadidae	*Myopholas multicostata* (AGASSIZ, 1842)
Pleuromyidae	*Pleuromya sinuosa* (ROEMER, 1839)
Laternulidae	*Cercomya* (*Capillimya*) *striata* AGASSIZ, 1844
	Plectomya rugosa (ROEMER, 1836)
Thraciidae	*Thracia incerta* (ROEMER, 1836)
?Cuspidariidae	?*Cuspidaria portlandica* (LORIOL, 1868)
Mactromyidae	*Mactromya concentrica* (MÜNSTER in GOLDFUSS, 1840)
	Unicardium crassum [MS CHOFFAT]

Family	**Species**
Megalodontidae	*Pachyrisma* sp.
	Pachyrismella sp. [Alves et al. 2003]
Diceratidae	*Plesiodiceras muensteri* (Goldfuss, 1840) [Alves et al. 2003]
	Diceratidae gen. et sp. indet. [Manuppella et al. 1999]
Sowerbyidae	*Sowerbya deshayesea* (Buvignier, 1851)
Tancrediidae	*Tancredia* (*Palaeomya*) *typica* (Roeder, 1882)
Gastrochaenidae	?*Gastrochaena* sp.
Arcticidae	*Anisocardia* (*Antiquicyprina*) sp.
	Isocyprina (*Venericyprina*) sp.
Neomiodontidae	*Neomiodon nuculaeformis* (Roemer, 1836)
	Eomiodon securiformis (Sharpe, 1850)
	Eomiodon sp.
	Myrene estremadurae Fürsich & Werner, 1985
	Myrene hannoverana Huckriede, 1967
Ceratomyopsidae	*Ceratomyopsis striata* (D'Orbigny, 1822)
Cardiidae	*Protocardia peraltaensis* Fürsich & Werner, 1985
	Protocardia intexta (Münster in Goldfuss, 1837)
	Protocardia semipunctata (Münster in Goldfuss, 1837)
	Protocardia gigantea Schneider, Werner & Fürsich, submitted
	Protocardia pesolina (Contejean, 1860)
	Tendagurium bannesianum (Contejean ex Thurmann, 1860)
Tellinoidea	"*Cardita*" *asteriana* Dollfus, 1863
Corbulidae	*Jurassicorbula viriati* Fürsich & Werner, 1985
	Jurassicorbula edwardi (Sharpe, 1850)
	Jurassicorbula inflexa (Roemer, 1836)
	Corbulomima suprajurensis (d'Orbigny, 1850)
	div. Heterodonta indet.

Tab. 1. Systematic list of Bivalvia from the Upper Jurassic of the Lusitanian Basin.

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SCHNEIDER, S., FÜRSICH, F.T. & WERNER, W. in press. Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. – International Journal of Earth Sciences. [DOI 10.1007/s00531-008-0359-3]

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Papers included in this Thesis

Paper 1

SCHNEIDER, S., FÜRSICH, F.T. & WERNER, W. in press. Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. – International Journal of Earth Sciences. [DOI 10.1007/s00531-008-0359-3]

Work performed by S.Schneider: Sample collection and preparation, data acquisition, figures and artwork, text writing and discussion (80%).

Paper 2

FÜRSICH, F.T., WERNER, W. & **SCHNEIDER, S.** accepted. Autochthonous to parautochthonous bivalve concentrations within transgressive marginal marine strata of the Upper Jurassic of Portugal. – Palaeobiodiversity and Palaeoenvironments.

Work performed by S.Schneider: Figures and artwork, text writing and discussion (20%).

Paper 3

SCHNEIDER, S., FÜRSICH, F.T., SCHULZ-MIRBACH, T. & WERNER, W. submitted: Ecophenotypic plasticity *versus* evolutionary trends – Morphological variability in Upper Jurassic bivalve shells from Portugal.

Work performed by S.Schneider: Sample collection (80%) and preparation, data acquisition, figures and artwork, morphometry and statistics (75%), text writing and discussion (80%).

Paper 4

SCHNEIDER, S., FÜRSICH, F.T. & WERNER, W. accepted. Marking the Kimmeridgian-Tithonian transition with a bivalve – *Protocardia gigantea* sp. nov. (Bivalvia: Cardiidae) and its relatives from the Lusitanian Basin (Portugal). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen.

Work performed by S.Schneider: Sample collection (50%) and preparation, data acquisition, figures and artwork except hand drawings, morphometry and statistics, text writing and discussion (80%).

Paper 5

SCHNEIDER, S., FÜRSICH, F.T. & WERNER, W. in preparation. A biometrically supported species concept for *Trigonia* BRUGUIÈRE (Bivalvia; Trigoniidae) and its application.

Work performed by S.Schneider: Sample collection (50%) and preparation, data acquisition, figures and artwork, morphometry and statistics, text writing and discussion (80%).

Paper 6

SCHNEIDER, S. & WERNER, W. 2007. Colour pattern preservation in *Fuersichella* n. gen. (Gastropoda: Neritopsoidea), bivalves, and echinid spines from the Upper Jurassic of Portugal. – Beringeria, **37**: 143-160.

Work performed by S.Schneider: Sample collection (50%) and preparation, data acquisition, figures and artwork, text writing and discussion (75%).

Int J Earth Sci (Geol Rundsch) (2009) 98:1949–1970
DOI 10.1007/s00531-008-0359-3

ORIGINAL PAPER

Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells

Simon Schneider · Franz T. Fürsich ·
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Received: 29 December 2007 / Accepted: 10 August 2008 /

Abstract Strontium isotope stratigraphy was performed on oyster shells from the Late Jurassic of the Lusitanian Basin (central Portugal). This represents the first approach to obtain numerical ages for these strata. The new chronostratigraphic data provide a more precise age determination of several units. After a basin-wide hiatus sedimentation in the Late Jurassic is proven in the Cabo Mondego and Cabaços formations to resume as early as the Middle Oxfordian. The Alcobaça formation can be placed in the latest Late Oxfordian to Late Kimmeridgian, while data from the upper part of the Abadia Formation indicate an Early to Late Kimmeridgian age. The Farta Pao formation ranges from the latest Kimmeridgian to the latest Tithonian. The largely synchronous Sobral, Arranhó I, and Arranhó II members are overlain by the late Early to Late Tithonian Freixial Member. The brief, local carbonate incursion of the Arranhó I member marks the Kimmeridgian–Tithonian boundary. Oysters are shown once more to be suitable for strontium isotope studies. Their calcitic shells are often unaffected by diagenesis. In particular for marginal marine Jurassic and Cretaceous strata, where belemnites are usually absent, oysters may serve as a valuable tool for isotope stratigraphy.

Keywords Oysters · Strontium isotopes · Stratigraphy · Upper Jurassic · Portugal

Introduction

Despite of more than 150 years of geological research, started by Sharpe in 1850, the stratigraphy and subdivision of the Upper Jurassic rocks of the Lusitanian Basin (central Portugal) are still muddled. This is mainly due to the lack of (bio-) stratigraphic markers. Large parts of the Upper Jurassic succession of the area consist of marginal-marine strata that often formed in low-salinity regimes. Consequently, the classical biostratigraphic indicators of the Jurassic, i.e. ammonites, are scarce or absent from those rocks. Moreover, ammonite stratigraphy is hampered by the palaeogeographic position of the Lusitanian Basin, which had a restricted access to the open Proto-Atlantic. Moreover, the basin occupied an intermediate position between the Boreal and Tethyan faunal provinces, resulting in a largely endemic ammonite fauna (e.g. Leinfelder et al. 2004). As ammonites are scarce or lacking, other macrofossils, such as bivalves and gastropods, were used besides lithological characteristics for stratigraphically subdividing the basin fill (Choffat 1885a, 1885–1888, 1887, 1893a, b, 1901, 1914; Sharpe 1850). However, most of these macrofossils were facies-controlled and therefore of only limited biostratigraphic value. The resulting scheme, refined by subsequent workers, is still partially in use. Moreover, the lithostratigraphic subdivision of the Upper Jurassic strata of the basin is far from resolved. For

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Palaeobio Palaeoenv (2009) 89:161–190
DOI 10.1007/s12549-009-0008-2

Autochthonous to parautochthonous bivalve concentrations within transgressive marginal marine strata of the Upper Jurassic of Portugal

Franz Theodor Fürsich · Winfried Werner · Simon Schneider

Received: 12 July 2009 / Revised: 9 September 2009 / Accepted: 14 September 2009 / Published online: 30 October 2009

Abstract Bivalve concentrations are a conspicuous feature of the Upper Jurassic rock succession of the central Lusitanian Basin. In order to illustrate the mode of their formation and their palaeoecological and sequence stratigraphic significance, we describe and interpret in detail 27 assemblages of bivalves based on their taphonomic and ecological features. Bivalve concentrations are particularly widespread in marginally marine, salinity-controlled environments and less common in open shelf settings. Only the *Eomiodon* and *Myophorella* concentrations are dominated by a shallow infaunal bivalve; all other concentrations are composed mainly of epi- or endobyssate [*Isognomon* (*Rostroperna*), *I.* (*Isognomon*), *Pteria*, *Alaperna*, *Juranomia*] and cementing taxa (*Praeexogyra*, *Actinostreon*). Most of the concentrations are mono- to paucispecific, except for the highly diverse *Alaperna polita–Pteria credneriana* concentrations, which occur in nearshore shelf environments. Lack of sorting, a high percentage of articulated shells, and shells preserved in growth position are evidence that, with few exceptions, the concentrations are autochthonous. Main factors leading to their formation are, apart from a gregarious life habit, a high productivity and a reduced rate of sedimentation. Autogenic and allogenic successional stages can be recognized on the basis of their spatial separation. The time involved in the formation of the concentrations is generally in the order of 10^2–10^3 years. Due to the lack of compositional changes within concentrations, time-averaging played no or only a minor role, except in the *Alaperna polita–Pteria credneriana* concentrations. In sequence stratigraphic terms, most of the concentrations are the product of the maximum flooding zone, but in some cases they constitute the transgressive systems tract. Invariably, they are useful tools for defining depositional sequences. Several of the concentrations described here are not restricted to the Lusitanian Basin but also occur elsewhere in the epicontinental seas bordering the northern margin of the Neotethys.

Keywords Bivalvia · Jurassic · Lumachelle · Palaeoecology · Sequence stratigraphy · Taphonomy

Introduction

Skeletal concentrations (Kidwell et al. 1986), also known as shell beds or lumachelles, by definition yield fossils in great profusion. However, often they cannot be used for palaeoecological analysis because they underwent a range of physical processes that distorted the composition of the original communities by modifying rank abundances, trophic proportions, and diversity values. In contrast, the taphonomic signatures of individual skeletal elements and the biofabric usually provide detailed information on the processes that led to the concentration of skeletal elements (e.g., Strauch 1990; Kidwell 1991; Fürsich and Oschmann

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Ecophenotypic plasticity *versus* evolutionary trends – Morphological variability in Upper Jurassic bivalve shells from Portugal

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Abstract

Upper Jurassic marginal marine strata of the Lusitanian Basin (central Portugal) yield a rich benthic macrofauna from which three bivalve target taxa, i.e. *Arcomytilus*, *Isognomon*, and *Eomiodon*, were chosen for morphometric studies, because of their abundance both in space and time and their variability in shell shape. The shells have been analysed with regard to outline shape (Fourier shape analysis), dimensions, ornamentation (*Arcomytilus*) and ligament arrangement (*Isognomon*). Additionally, data on co-occurring fauna and palaeotemperatures calculated from $\delta^{18}O$ values have been recorded. The results of the morphometric analyses have been interpreted with regard to phylogeny and palaeoecology. In all target taxa, a distinct, rapid size increase at around the Early/Late Kimmeridgian boundary is evident. Potential causes for this process are discussed, and an increase in food availability is regarded the most likely scenario. In *Isognomon rugosus* (Münster in Goldfuss, 1835), a distinct change in resilifer arrangement co-occurs with size increase, resulting in the evolution of an endemic species in the Lusitanian Basin, for which the name *Isognomon lusitanicus* (Sharpe, 1850) is re-established. Like in several extant Mytilidae, morphological species characterisation in *Arcomytilus* turns out unsatisfactory, due to high intra-specific variability. However, *Arcomytilus morrisii* (Sharpe, 1850) is still regarded as a valid species that evolved in the Lusitanian Basin. Despite of shape variability *Eomiodon securiformis* (Sharpe, 1850) is also considered to be a clearly distinguished species. For all target taxa morphologic variability is discussed with regard to environment, and variation between populations is delineated. The data suggest a weak correlation of facies and shell shape in *Arcomytilus*, while *Isognomon lusitanicus* seems to develop local varieties in different subbasins. Finally, the great morphologic plasticity of bivalves from rather distinct systematic entities is shown to result from different causes, thus demonstrating that careful studies of the involved species is a prerequisite to draw correct palaeoecological conclusions.

Key words: Bivalvia, Late Jurassic, Portugal, morphometry, Fourier shape analysis, size increase, ecophenotypy, phylogeny.

Marking the Kimmeridgian-Tithonian transition with a bivalve – *Protocardia gigantea* sp. nov. (Bivalvia: Cardiidae) and its relatives from the Lusitanian Basin (Portugal)

Simon Schneider, München, **Franz T. Fürsich**, Erlangen, and **Winfried Werner**, München

With 9 figures

Schneider, S., Fürsich, F. T. & Werner, W. (20XX): Marking the Kimmeridgian-Tithonian transition with a bivalve – *Protocardia gigantea* sp. nov. (Bivalvia: Cardiidae) and its relatives from the Lusitanian Basin (Portugal). – N. Jb. Geol. Paläont. Abh., **XXX**: 00-00; Stuttgart.

Abstract

The cardiid *Protocardia gigantea* sp. nov., which is newly described herein, represents the largest member of this globally distributed genus of shallow-water Mesozoic bivalves. It is found throughout the central Lusitanian Basin (Central Portugal) and may be utilised as a stratigraphic marker for the Kimmeridgian-Tithonian transition in this area, which is confirmed by Sr-isotope data. Its frequent occurrence, large size, and characteristic features make *Protocardia gigantea* a valuable tool for field stratigraphy. Its taxonomy, systematic position, and ontogenetic as well as intra-population morphological variability are outlined. Possible ancestry in and outside the Lusitanian Basin is discussed, and four other species of *Protocardia* from the Upper Jurassic of Portugal are taxonomically treated.

Key words: *Protocardia*, Cardiidae, stratigraphy, Late Jurassic, Portugal, taxonomy, morphometry, Fourier shape analysis.

1. Introduction

Although bivalves are among the most frequently occurring benthic invertebrates at least since the Late Palaeozoic (MILLER & SEPKOSKI 1988, CLAPHAM et al. 2006), their biostratigraphic value is, with a few exceptions such as inoceramids and buchiids, relatively low (AMLER et al. 2000). This is due to usually low evolutionary rates and a large proportion of analogous morphological adaptations. In marine Mesozoic strata, bivalves are usually accompanied by the much faster evolving ammonites, which represent excellent tools for relative dating. From most Upper Jurassic rocks of the Lusitanian Basin (Central Portugal), however, ammonites are virtually absent, due to the semi-enclosed palaeogeographic position

Simon Schneider[1*], Franz Theodor Fürsich[2] and Winfried Werner[1, 3]

A biometrically supported species concept for *Trigonia* BRUGUIÈRE (Bivalvia; Trigoniidae) and its application

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Abstract

From its first occurrence in the Middle Triassic to the Late Cretaceous, and thus for almost 200 Ma, *Trigonia*, type genus of the family Trigoniidae, became established as a frequent constituent of global shallow marine benthic faunas. Despite of its abundance, however, *Trigonia* is still highly over-splitted at species level, which hampers sound biostratigraphic, palaeobiogeographic and palaeoecologic applications. The present study focuses on two closely related species, i.e. *Trigonia reticulata* AGASSIZ and *Trigonia pseudomeriani* CHOFFAT, and illustrates typical problems of species identification in this genus. *T. reticulata* is a well-known representative of the genus with a significant fossil record in Lower Oxfordian to Upper Kimmeridgian strata of western and central Europe, and likely is the ancestor of *T. pseudomeriani*, which is endemic to the Upper Oxfordian to Lower Kimmeridgian Alcobaça formation of the Lusitanian Basin (central Portugal). Besides classical qualitative taxonomy, a set of metric and non-metric parameters are captured and outlines are digitally analyzed from a representative number of specimens from different localities and stages to address intraspecific variability. The results are interpreted with regard to palaeoecology and palaeobiogeography and a modern species concept for *Trigonia* is proposed that may be successfully applied to other members of the Trigoniinae as well. In addition, the global distribution of the genus *Trigonia* is surveyed in five time slices and the potential origins of the resulting patterns are discussed.

Key words: *Trigonia*, Trigoniidae, bivalves, Fourier shape analysis, morphometry, Late Jurassic, Portugal.

Colour pattern preservation in *Fuersichella* n. gen. (Gastropoda: Neritopsoidea), bivalves, and echinid spines from the Upper Jurassic of Portugal

SIMON SCHNEIDER & WINFRIED WERNER

SCHNEIDER, S. & WERNER, W. 2007. Colour pattern preservation in *Fuersichella* n. gen. (Gastropoda: Neritopsoidea), bivalves, and echinid spines from the Upper Jurassic of Portugal. – Beringeria **37**: 143-160, 10 text-figs.; Würzburg.

Abstract. Colour preservation has been observed in shells and spines of five different invertebrate taxa from the Upper Jurassic of the Lusitanian Basin, Portugal. In this paper the colour patterns of these animals are detailed; moreover, the neritimorph gastropod „*Neritina*“ *bicornis* is placed in the new genus *Fuersichella*. Coloured bands in the shell of the bivalve *Isognomon rugosus* are documented for the first time. Newly discovered material provides additional information on the morphology and colouration of *Coelastarte discus*. In addition, the first detailed characterization of the colour patterns preserved in fossil echinoid spines assignable to *Pseudocidaris lusitanica* and *P. spinosa* is given. Finally, chemical composition, formation, and possible functions of the colour patterns in these animals are discussed.

■ *Colour patterns, Bivalvia, Gastropoda, Echinoidea, Late Jurassic, Portugal*

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Introduction

Our most sophisticated sense organs are the eyes. Through the eyes, we are visually attracted to two fundamental parameters of the objects: shape and colour. While shape is critical in the analysis of virtually all fossils, colour is rarely preserved, and thus has attracted the attention of palaeontologists since the late 18th century (BRUGUIÉRE 1792). Today, there exists an extensive body of literature addressing colour preservation in a wide variety of fossil invertebrates (e.g. HOARE 1978, MAPES & HOARE 1987).

Secretion of inorganic and/or organic hard-parts while the animal is alive is usually a prerequisite for colour preservation in fossils. Most coloured fossils represent calcareous skeletons, predominantly those of molluscs. A variety of colour patterns and modes of preservation have been documented for polyplacophorans (e.g. HOARE & SMITH 1984, HOARE et al. 2002), bivalves (e.g. NUTTALL 1969, KOBLUK & MAPES 1989), nautilids (e.g. FOERSTE 1930, KOBLUK & MAPES 1989), ammonites (e.g. MAPES & SNECK 1987, MAPES & DAVIS 1996), belemnites (JORDAN et al. 1975, SPÄTH 1983), and, most important, gastropods (e.g. KOBLUK & MAPES 1989, TICHY 1980). The second largest group of coloured shell-bearing fossils are the brachiopods (e.g. FOERSTE 1930, KOBLUK & MAPES 1989). Colour preservation in echinoderms is known to occur in blastoids (e.g. REIMANN 1961, BEAVER & FABIAN 1998), cystoids (PAUL 1967), crinoids (e.g. BLUMER 1960, 1965, WOLKENSTEIN et al. 2006), and echinids (COTTEAU 1881, KROH 2003, HOSTETTLER 2006). Coloured carapaces of trilobites (see KOBLUK & MAPES 1989 for a review), phyllocarids (STUMM & CHILMAN 1969), and cirripeds (e.g. YAMAGUCHI 1980) are examples for colour preservation in fossil crustaceans. Last but not least, the chitinous carapaces of insects may retain colour, if preserved in conservation-type Lagerstätten (see HOARE 1978 and MAPES & HOARE 1987 for examples).

Trilobites from the Cambrian are the oldest organisms known to date to display colour patterns (RAYMOND 1922). Early coloured nautiloids (e.g. MARSH 1869, KOBLUK & HALL 1976), brachiopods (SINGH 1979), and gastropods (WHITE 1896, RAYMOND 1906) have been reported from

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1998–2004: University studies in geology and paleontology, Ludwig-Maximilians-Universität München, Germany
2000: Four-week internship, Naturmuseum Augsburg, Germany; re-organization of mollusc collection and preparation of exhibitions
September 2000: Vordiplom in geology and paleontology, Ludwig-Maximilians-Universität München, Germany
2001: Three-week internship, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; scientific excavation at Miocene vertebrate locality Sandelzhausen
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Positions held

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2004-2007: Research assistant, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; Project: DFG - FU 131/31-2, and WE 1152/2-2): Speziation oder Ökophänotypie? Analyse morphologischer Veränderungen oberjurassischer Bivalven aus dem Lusitanischen Becken (Portugal). Advisors: Prof. Dr. F. T. Fürsich (Institut für Geologie und Paläontologie der Universität Würzburg, Germany) and Dr. W. Werner (Bayerische Staatssammlung für Paläontologie und Geologie, München).

Current Position

Acting librarian at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, since April 2008.

Professional Affiliations

Paläontologische Gesellschaft
Werkgroep voor Tertiaire en Kwartaire Geologie

Theses

2003: Paläoökologische Untersuchungen an Bivalven aus dem Oberjura von Portugal mit Hilfe stabiler Isotope. 47 pp.

Diploma Thesis submitted in partial fulfillment of the requirements for the diploma degree of the Faculty of Geosciences, Ludwig-Maximilians-Universität München, Germany. Advisors: Prof. Dr. R. R. Leinfelder (Department for Geo- and Environmental Sciences, München) and Dr. W. Werner (Bayerische Staatssammlung für Paläontologie und Geologie, München) [unpublished]

2003: Geologische Kartierung von Weissenbrunn/Seibelsdorf (Oberfranken). 36 pp. + map.

Thesis and geological map submitted in partial fulfillment of the requirements for the diploma degree of the Faculty of Geosciences, Ludwig-Maximilians-Universität München, Germany. Advisors: Prof. Dr. R. R. Leinfelder, Dr. D. Schmid (both Department for Geo- and Environmental Sciences, München) and Dr. M. Nose (Bayerische Staatssammlung für Paläontologie und Geologie, München) [unpublished]

List of Publications

Scientific publications

Papers included in the thesis are indicated by an asterisk.

2009:

NIEBUHR, B. & **SCHNEIDER, S.** (2009): (9) Sandbach-Formation. – In: NIEBUHR, B., PÜRNER, T. & WILMSEN, M.: Lithostratigraphie der außeralpinen Kreide Bayerns. – Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften e.V., **65**: 36-38. [13]

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2008:

LIGNEREUX, Y., MANHART, H. & **SCHNEIDER, S.** (2008): Les restes animaux du Palais d'Amathonte à Chypre, à l'Époque classique (Ve et IVe siècles av. J.-C.). In: VILA, E., GOURICHON, L., CHOYKE, E. M. & BUITENHUIS, H.: Proceedings of the 8th International Symposium on the Archaeozoology of southwestern Asia and adjacent areas, part 2. – Travaux de la maison de l'Orient et de la Méditerranée, **49**: 597-628. [11]

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2007:

FÜRSICH, F. T., WERNER, W., **SCHNEIDER, S.** & MÄUSER, M. (2007): Sedimentology, taphonomy, and palaeoecology of a laminated plattenkalk from the Kimmeridgian of the northern Franconian Alb (southern Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology, **243**: 92-117. [6]

***SCHNEIDER, S.** & WERNER, W. (2007): Colour pattern preservation in *Fuersichella* n. gen. (Gastropoda: Neritopsoidea), bivalves, and echinid spines from the Upper Jurassic of Portugal. – Beringeria, **37**: 143-160. [5]

FÜRSICH, F. T., MÄUSER, M., **SCHNEIDER, S.** & WERNER, W. (2007): The Wattendorf Plattenkalk (Upper Kimmeridgian) - a new conservation lagerstätte from the northern Franconian Alb, southern Germany. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **245** (1): 45-58. [4]

2006:

SCHNEIDER, S. & SELMEIER, A. (2006): A silicified wood from the church of St. Laurentius in Zeholfing (Bavaria, Germany) – an unusual link between archeology and paleontology. – Zitteliana, **A46**: 105-109. [3]

2005:

SCHNEIDER, S., WITT, W. & YIGITBAŞ, E. (2005): Ostracods and bivalves from an Upper Pleistocene (Tyrrhenian) marine terrace near Altınova (İzmit Province, Turkey). – Zitteliana, **A45**: 87-114. [2]

SCHNEIDER, S. & HEISSIG, K. (2005): An early seal (Mammalia, Pinnipedia) from the Middle Miocene (Langhian) of Miste (The Netherlands). – Scripta Geologica, **129**: 151-158. [1]

In press:

***SCHNEIDER, S.**, FÜRSICH, F. T. & WERNER, W. (in press): Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. – International Journal of Earth Sciences.

BITNER, A. M. & **SCHNEIDER, S.** (2009): The Late Burdigalian (Ottnangian) brachiopod fauna from the northern coast of the Upper Marine Molasse Sea in Bavaria, Southern Germany. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **254**: 117-133.

JÄGER, M. & **SCHNEIDER, S.** (2009): Serpulidae (Annelida, Polychaeta) from the Lower Ottnangian (Late Burdigalian) Upper Marine Molasse of Dommelstadl and Gurlarn (Passau area, Lower Bavaria, SE Germany). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **254**: 105-115.

SCHNEIDER, S., BERNING, B., BITNER, M. A., CARRIOL, R-P., JÄGER, M., KRIWET, J., KROH, A. & WERNER, W. (2009): A parautochthonous shallow marine fauna from the Late Burdigalian (early Ottnangian) of Gurlarn (Lower Bavaria, SE Germany): Macrofaunal inventory and paleoecology. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **254**: 63-103.

Accepted:

***SCHNEIDER, S.**, FÜRSICH, F. T. & WERNER, W.: Marking the Kimmeridgian-Tithonian transition with a bivalve – *Protocardia gigantea* sp. nov. (Bivalvia: Cardiidae) and its relatives from the Lusitanian Basin (Portugal). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen.

*FÜRSICH, F. T., WERNER, W. & **SCHNEIDER, S.**: Autochthonous to parautochthonous bivalve concentrations within transgressive marginal marine strata of the Upper Jurassic of Portugal. – Palaeobiodiversity and Palaeoenvironments.

Submitted:

***SCHNEIDER, S.**, FÜRSICH, F. T., SCHULZ-MIRBACH, T. & WERNER, W.: Ecophenotypic plasticity *versus* evolutionary trends – Morphological variability in Upper Jurassic bivalve shells from Portugal.

BÖHME, M., PRIETO, J., **SCHNEIDER, S.**, HUNG, N. V., QUANG, D. D., TRAN, D. N.: The Cenozoic on-shore basins of Northern Vietnam: biostratigraphy, vertebrate and invertebrate faunas.

In preparation:

***SCHNEIDER, S.**, FÜRSICH, F. T. & WERNER, W.: A biometrically supported species concept for *Trigonia* BRUGUIÈRE (Bivalvia; Trigoniidae) and its application.

FÜRSICH, F. T., WERNER, W. & **SCHNEIDER, S.**: The macrofauna of the Wattendorf Plattenkalk. Part 1: Bivalvia and Gastropoda.

Miscellanea (Popular Articles, Notes, Brochures, etc.)

2009:

AMLER, M. R. W. & **SCHNEIDER, S.** (2009): Fossil des Monats Januar 2009: Rostroconchier *Apotocardium lanterna* (BRANSON, 1965). – BSPG München, flyer. [17]

2008:

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