



Morphology and Phylogeny
of Synechodontiform Sharks
(Chondrichthyes, Elasmobranchii)
with Comments on the Origin and
Early Evolution of Neoselachii

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and Early Evolution of Neoselachii

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*To my family
for their permanent support,
continuous encouragement
and always believing in me*

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Zusammenfassung

Diese Doktorarbeit ist das Resultat von drei Jahren intensiver Forschung über eine Gruppe ausgestorbener Haifische, die allgemein unter dem Namen *Synechodontiformes* bekannt ist. Mit dem Ziel, sowohl ihre Phylogenie und Evolution zu rekonstruieren, als auch ihre systematische Position innerhalb der Knorpelfische und ihrer Beziehungen zu den modernen Haien und Rochen (Neoselachii) zu identifizieren, wurde eine ausführliche Studie der skelettalen Überreste und isolierten Zähne durchgeführt. Diese Hai-Gruppe ist vollständig ausgestorben, wobei die frühesten Vertreter aus dem Perm bekannt sind und die letzten aus dem Eozän.

In den letzten Jahrzehnten wurde teilweise vehement über die Monophylie der *Synechodontiformes* und ihre Stellung innerhalb der Neoselachier diskutiert. Dies ist in erster Linie dadurch begründet, dass nur sehr wenige skelettale Reste bekannt waren. Zusätzlich sind die Zähne der einzelnen Gattungen, die traditionell den *Synechodontiformes* zugeordnet werden, in ihrer Morphologie sehr ähnlich, so dass es kaum möglich war, verwertbare Merkmale für phylogenetische Analysen zu identifizieren. Aufgrund dessen wurden unterschiedliche Klassifikationen vorgeschlagen, die sich mitunter deutlich widersprachen.

Die taxonomische und systematische Revision führte im Verlauf dieser Studie zu der Einführung einer neuen Gattung – *Palidiplospinax* – basierend auf skelettalen Überresten. Diese Gattung umfasst kleine Haie mit zwei Rückenflossen, die durch Stacheln gestützt werden. Exemplare dieses Taxons finden sich hauptsächlich in unter- und mitteljurassischen Ablagerungen Europas. Die Revision der Neoselachier-Skelette aus den oberjurassischen lithographischen Plattenkalken Solnhofens und Nusplingens lieferte die ersten Skelette von *Synechodus* aus dem Oberjura, die eine neue Art repräsentieren – *Synechodus ungeri*. *Synechodus* war bisher nur durch sehr fragmentarische Skelettreste aus der Oberkreide bekannt. Zusätzlich erbrachte die Revision einige nahezu vollständige Skelette adulter und juveniler Exemplare von *Paraorthacodus jurensis*, der bis dato lediglich durch den unvollständigen Holotypen belegt war.

Diese neuen Exemplare und Taxa führten zu der Erkenntnis, dass *synechodontiforme* Haie im Jura viel zahlreicher und diverser waren als bisher angenommen. Der kleine Haifisch, *Macrourogaleus*, ehemals zu den Katzenhaien gestellt, wird als nächster Verwandter zu *Paraorthacodus* identifiziert. Zusätzlich wird das erste komplette Skelett von *Paraorthacodus jurensis* beschrieben, das detaillierte Informationen für die Anatomie dieser Haifische liefert. Der deutlichste Unterschied zwischen *Paraorthacodus* und *Synechodus*, der aufgrund dieser Revision

festgestellt werden konnte, ist, dass *Paraorthacodus* eine einzelne Rückenflosse hat, während *Synechodus* zwei aufweist. Der Hauptunterschied zwischen diesen beiden Taxa und *Palidiplospinax* ist der Besitz von Flossenstacheln des letzteren vor den Rückenflossen.

Diese Revision ermöglichte eine Analyse der taxonomischen Vielfalt der oberkretazischen synechodontiformen Haie Gondwanas, die im Vergleich zu Europa nur unzureichend dokumentiert ist, was im Wesentlichen an der ausgeprägten Sammeltradition in Europa liegt. Das Hauptaugenmerk galt hierbei der antarktischen Fauna.

Die phylogenetischen Analysen, die im Rahmen dieser Arbeit durchgeführt wurden, um die Monophylie der Synechodontiformes als auch ihre Stellung innerhalb des Systems der Knorpelfische zu rekonstruieren, basiert ausschließlich auf morphologischen Merkmalen. Auch wenn molekulare Datensätze in zunehmendem Maße vorhanden und zugänglich sind, wurden sie nicht miteinbezogen entsprechend dem ausschließlich fossilen Auftreten von synechodontiformen Haien. Vier verschiedene Analysen wurden durchgeführt und führten unter anderem zu der Schlussfolgerung, dass alle einbezogenen Gattungen, die traditionell zu den Synechodontiformes gestellt werden, tatsächlich eine sehr gut gestützte monophyletische Gruppe bilden, die die basale Schwestergruppe zu allen anderen Neoselachii darstellt. Dies führt zu der Schlussfolgerung, dass das systematische Konzept der Neoselachii erweitert werden muss, um auch ausgestorbene Gruppen mit einzubeziehen, die phylogenetisch nicht innerhalb der Neoselachii angesiedelt sind. Die Verwandtschaftsverhältnisse der Innengruppe der Synechodontiformes bleiben zum Teil unaufgelöst, da einige Gattungen nur auf isolierten Zähnen basieren und deren Datensätze entsprechend eingeschränkt sind. Vier gut begründete monophyletische Gruppierungen einschließlich einer neuen Familie – *Paraorthacodontidae* (aus *Macrourogaleus* und *Paraorthacodus* bestehend) – können auf Grund der kladistischen Analyse unterschieden werden.

Die neuen, durch diese Studie erbrachten Ergebnisse ermöglichten Diversifizierungs- und biogeographische Muster während des Jura statistisch zu analysieren und den Zeitpunkt des ersten wichtigen Diversifikationsereignisses der Neoselachii zu rekonstruieren. Die wichtigsten Resultate dieser beiden Analysen sind zum einen, dass die maximale Diversifizierungsrate im Toarc (ca. 180 Ma) stattfand und sich auf einem gleichmäßigen Level im Mittel- und Oberjura einpendelte, und zum anderen, dass das stets angenommene Aussterbeereignis am Ende des Jura eher ein Artefakt ist als ein reales Muster darstellt.

Abstract

This dissertation is the result of three years of research into a group of extinct sharks collectively known as *Synechodontiformes*. In an effort to reconstruct their phylogeny and evolution and to identify their position within cartilaginous fishes and their relations to modern sharks, rays and skates (*Neoselachii*) a detailed study of skeletal remains and isolated teeth was carried out. This group is exclusively fossil without any extant representatives ranging from the Late Permian to the Palaeocene. The different views about their relationships to other elasmobranchs and interrelationships of taxa assigned to this group resulted in major controversies in recent decades because of very rare skeletal remains and very similar dental morphologies in closely related genera. Different systematic concepts were proposed, which, however, not have been tested using cladistic principles up to now.

The taxonomic and systematic revisions performed in the course of this study resulted in the recognition of a new genus, *Palidiplospinax*, based on skeletal remains, which comprises small Early Jurassic sharks characterized by two dorsal fins supported by spines. Remains of this genus are common in Early and Middle Jurassic deposits in Europe. The revision of neoselachian skeletons from the Upper Jurassic lithographic limestones of the Solnhofen area and Nusplingen yielded the first skeletons of Late Jurassic *Synechodus* including a new species, *Synechodus ungeri*. *Synechodus* was represented by very fragmentary skeletal remains from the Late Cretaceous so far. In addition, the revision yielded several complete skeletons of adult and juvenile individuals of *Paraorthacodus jurensis*, which has been known exclusively from the very incomplete holotype up to now.

These new specimens and taxa resulted in the perception that *synechodontiform* sharks were more abundant and diversified during the Jurassic than previously assumed. The small shark, *Macrourogaleus*, previously considered a cat shark, is identified as closely related to *Paraorthacodus*. Additionally, the first complete skeleton of *Paraorthacodus jurensis* is described providing detailed information on the anatomy of these sharks. The most conspicuous differences between *Paraorthacodus* and *Synechodus*, which were possible to be established with the new material, is that *Paraorthacodus* has a single dorsal fin, whereas *Synechodus* has two dorsal fins. Differences between these two taxa and *Palidiplospinax* include the presence of dorsal fin spines in the latter.

In a next step, the taxonomic diversity of Late Cretaceous *synechodontiforms* from Gondwana with special reference to Antarctic taxa was established because

the fossil record of synechodontiforms is highly biased towards Europe. This is mainly due to the longer collecting tradition in Europe.

In the course of these taxonomic revisions, abundant dental and skeletal data of synechodontiform taxa were accumulated for a subsequent phylogenetic analysis employing robust cladistic principles and a group of completely extinct taxa for the first time. The data set based on morphological characters includes a combination of previously published information and new data. Although molecular sequences are increasingly abundant and accessible, they were not considered according to the exclusively extinct occur of synechodontiforms without the possibility to perform molecular analyses. Four different analyses were performed resulting in that Synechodontiformes form a monophyletic group, which is well-supported by a suite of characters and which is the basal sister group to all other neoselachians. This indicates that the systematic concept of Neoselachii must be expanded to include extinct groups that are not nested phylogenetically within Neoselachii. The ingroup interrelationships of Synechodontiformes remain largely unresolved due to the fact that several genera are only based on isolated teeth and the data set is rather restricted. It is possible to identify four cladistically well-supported monophyletic groupings including one new family, Paraorthacodontidae consisting of *Macrourogaleus* and *Paraorthacodus*.

The new data obtained from this study enabled to review diversity and bio-geographic patterns during the Jurassic as well as the timing of the first major diversification event of neoselachians in general employing statistical procedures. The most important results from these two analyses are that a first maximum of diversification is recognizable at the end of the Early Jurassic (Toarc; 180 Ma) resulting in a Middle and Late Jurassic plateau and that the assumed extinction at the end of the Jurassic represents an artefact rather than a real pattern.

Introduction

All modern sharks, skates and rays, and those extinct taxa nested phylogenetically within modern clades are collectively called Neoselachii and constitute a well-defined monophyletic clade [Euselachii of MOY-THOMAS (1939), SCHAEFFER & WILLIAMS (1977) and REIF (1977); Euselachiformes of MAISEY (1975)]. This highly diverse group is well supported by both morphological and molecular data and represents one of the most successful clades of chondrichthyan (cartilaginous) fishes. The most important period in the evolution of modern sharks, batoids and also bony fishes, was the Mesozoic, especially the Jurassic, because their origin and first major radiation events occurred during this time span (MAISEY *et al.* 2004; UNDERWOOD 2006; KRIWET & KLUG in press). All major clades of modern neoselachians are seemingly present in the Late Jurassic (e.g. THIOLLIÈRE 1854; SAINT-SEINE 1949; BEAUMONT 1960a, b; SCHWEIZER 1964; CAPPETTA 1987; THIES 1992; DUFFIN & WARD 1993; CAVIN *et al.* 1995; BRITO & SERET 1996; LEIDNER & THIES 1999; KRIWET & KLUG 2004, 2008; KRIWET *et al.* 2008). Nevertheless, our understanding of early neoselachian diversities, taxonomies, and systematics are still very inadequate despite many recent achievements (e.g. THIES & CANDONI 1998; LEIDNER & THIES 1999; BÖTTCHER & DUFFIN 2000; DELSATE & CANDONI 2001; UNDERWOOD 2002; KRIWET 2003a, b; KRIWET & BENTON 2004; KRIWET & KLUG 2004; MAISEY *et al.* 2004; UNDERWOOD & WARD 2004a, b; UNDERWOOD 2006). This is mainly related to the nature of preservation, because neoselachian skeletons are mostly cartilaginous and consequently become scarcely and only under exceptional taphonomic conditions fossilized. Isolated material, such as teeth, placoid scales or fin spines, conversely, is quite resistant and very abundant as fossils (e.g. CAPPETTA 1987; KRIWET 2004, 2005, 2006; HERMAN 1977; LEIDNER & THIES 1999; REES 2005; UNDERWOOD & WARD 2004a,b, 2008; KRIWET *et al.* in press). Neoselachian teeth are generally considered to be useful for taxonomic purposes similar to the condition in fossil mammals. Similar trophic adaptations, however, might result in similar tooth morphologies in not closely related groups. Moreover, many extinct and extant taxa show different degrees of ontogenetic and sexual dental variability (e.g. HERMAN *et al.* 1991, and other studies by these authors; KAJIURA & TRICAS 1996; SÁEZ & LAMILLA 1997, 2004; STRAUBE *et al.* 2008; UNDERWOOD & WARD 2008). The precise study of tooth morphologies in combination with fossilized skeletal elements is mostly the only way to establish systematically useful tooth characters for inferring interrelationships and diversity patterns through time. However, fossil localities with skeletal remains of neoselachians are very scarce. So far, skeletal remains of neoselachians have been reported mainly from the Jurassic of south-eastern France (THIOLLIÈRE 1854; SAINT-SEINE 1949), southern Germany (e.g. SCHWEIZER 1964; KRIWET & KLUG

2004; THIES 2005) and southern England (e.g. MAISEY 1977; DUFFIN & WARD 1993).

These skeletal remains are of utmost importance because they provide new insights into morphological traits, the early evolution and origins of neoselachians. Among the wide array of fossil neoselachian taxa reported from the Early Jurassic (e.g. WOODWARD 1895; DUFFIN & WARD 1993) and Late Jurassic (e.g. BÖTTCHER & DUFFIN 2000; KRIWET & KLUG 2004) is one group of sharks, the Synechodontiformes, which includes abundant taxa based on isolated teeth. Ranging from the Late Permian to the Palaeocene, they so far have been reported mostly from the Northern Hemisphere (CAPPETTA 1973, 1992; DUFFIN 1982, 1987, 1993a, b, c; BIDDLE 1993; CVANCARA & HOGANSON 1993; JOHNS *et al.* 1997; UNDERWOOD 2002; KRIWET 2003a; UNDERWOOD & WARD 2004a, b; KRIWET & KLUG 2004; IVANOV 2005), whereas only a few records are known from the Southern Hemisphere, which represents a quite deficient fossil record in these regions (DAVIS 1888; AMEGHINO 1893; KEMP 1991; KRIWET 2003b; RICHTER & WARD 1990; SIVERSON 1997). Synechodontiformes include traditionally eight genera. The taxon "*Palaeospinax*" EGERTON, 1872 is not considered valid according to DUFFIN & WARD (1993). In addition to two taxa with unclear affinities within Synechodontiformes (*Mucrovenator* CUNY *et al.*, 2001; *Rhomphaiodon* DUFFIN, 1993b), these sharks are traditionally arranged into three families, the Orthacodontidae BEAUMONT, 1960a (including *Sphenodus* AGASSIZ, 1843), Pseudonotidanidae UNDERWOOD & WARD, 2004a (including *Pseudonotidanus* UNDERWOOD & WARD, 2004a and *Welcommia* CAPPETTA, 1990) and Palaeospinacidae REGAN, 1906 (including *Paraorthacodus* GLIKMAN, 1957; *Synechodus* WOODWARD, 1888 and "*Palaeospinax*" EGERTON, 1872). The family Palaeospinacidae is the most diverse group with more than 30 described species. Up to now, the only skeletal remains of synechodontiforms known are from the Lower Jurassic ("*Palaeospinax*") and Upper Cretaceous (*Synechodus*) of England (e.g. MACKIE 1863; MAISEY 1985), and the Lower Jurassic ("*Palaeospinax*", *Pseudonotidanus*) and Upper Jurassic (*Sphenodus*, *Paraorthacodus*) of southern Germany (e.g. DUFFIN & WARD 1993; KRIWET & KLUG 2004). The scarcity of skeletal remains and the lacking comparability to living representatives causes major controversies related to the question if Synechodontiformes constitute a monophyletic group (that is sharing a common ancestors) and the confusing and debated taxonomy of Palaeospinacidae for many decades (e.g. DUFFIN & WARD 1993; MAISEY *et al.* 2004). The review of the neoselachian association from the Upper Jurassic lithographic limestones of southern Germany by KRIWET & KLUG (2004) entailed a comprehensive study of skeletal remains in different collections all over Europe. This review yielded several, up to now, undescribed or deceptively assigned skeletal remains of generally very small sharks including hitherto unknown

specimens of synechodontiforms that enable to overcome many controversies in synechodontiform taxonomy and systematics.

The intentions of this doctoral thesis are to (1) revise skeletal remains of synechodontiforms, especially palaeospinacids, from Jurassic deposits of Europe; (2) provide detailed morphological descriptions of palaeospinacid skeletons; (3) assign new taxa to the family Palaeospinacidae; (4) establish skeletal and dental characters for distinguishing "*Paleospinax*", *Paraorthacodus*, *Synechodus* and "*Synechodus*" *prorogatus*; (5) provide new information on the diversity and taxonomy of synechodontiforms from the Southern Hemisphere; (6) determine a phylogenetic analysis using robust cladistic principles testing the monophyly and systematic position of Synechodontiformes within Neoselachii and to re-evaluate the interrelationships of synechodontiform genera; and (7) analyse new information on the diversity of Jurassic synechodontiform sharks to provide an updated taxonomic database of neoselachian occurrences for performing analyses on diversification patterns of early sharks and rays employing sub-sampling methods.

Taxonomic and Systematic Background

Neoselachii

Neoselachii include all extant sharks and batoids (skates and rays) as well as a vast number of fossil taxa. They are divided into 14 orders that are arranged into three supraordinal groups (Galeomorphii, Squalomorphii, Batoidea). Living sharks comprise over 498 species (COMPAGNO *et al.* 2005) and living batoids (rays and skates) account for 574 species (EBERT & COMPAGNO 2007). Even though the monophyly of Neoselachii is beyond dispute, the diagnosis of this group varies and their interrelationships have been continuously discussed in the past (e.g. COMPAGNO 1973, 1977; MAISEY 1984a, b, 1986; THIES & REIF 1985; DINGERKUS 1986; GAUDIN 1991; SHIRAI 1992a, b, 1996; CARVALHO 1996; MAISEY *et al.* 2004). Some of the main controversies seemed to be settled by now. However, a comprehensive phylogeny of neoselachians that identifies the systematic position of problematic taxa such as Batoidea, Squaliformes (dogfishes), and Hexanchiformes (cow sharks), is still lacking (e.g. MAISEY *et al.* 2004). Unfortunately, most phylogenetic analyses based on cladistic principles employing molecular or morphological data encompass only a restricted number of taxa and data respectively, or result in different taxonomic arrangements. Morphological data suggest that batoids, i. e., are positioned high within Squalomorphii as derived sharks, joined with saw sharks and angel sharks

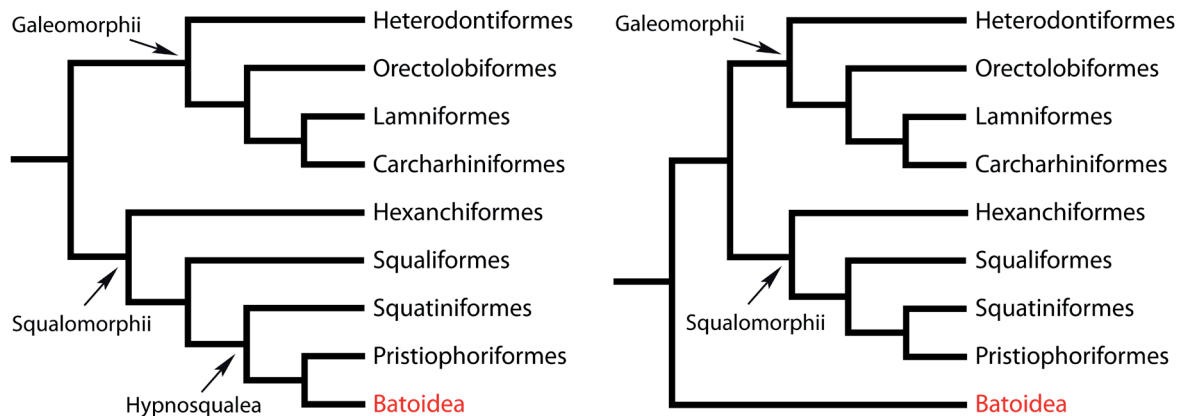


Figure 1. Phylogenetic hypotheses of Neoselachii. **A.** Batoidea as derived sharks within Squalomorpii as sister group to Pristiophoriformes (CARVALHO 1996; CARVALHO & MAISEY 1996; SHIRAI 1996). **B.** Batoids as sister group to all other modern sharks (e.g. WINCHELL *et al.* 2004).

in a clade Hypnosqualea (SHIRAI 1992b; CARVALHO 1996; CARVALHO & MAISEY 1996; Fig. 1A). Molecular analyses using larger sets of gene sequences conversely support the position of batoids as sister group basal to all sharks (DOUADY *et al.* 2003; WINCHELL *et al.* 2004; Fig. 1B). This interpretation also is supported by the fact that molecular phylogenies are more congruent with the fossil record, whereas morphological phylogenetic hypotheses (e.g. CARVALHO 1996) require long ghost-lineages to be congruent with the fossil record (see chapter “Results and Conclusions”). All information published so far indicates that the monophyly and interrelationships of Squaliformes (dogfishes), the identity and systematic position of Hexanchiformes (cow sharks) and Scyliorhinidae (cat harks) within Neoselachii, for instance, are in urgent need of re-examination and consequently still are debated (e.g. MAISEY 1980; SHIRAI 1992a, 1996; CARVALHO 1996). The interrelationships of neoselachians at genus and species level also are not fully resolved and almost all fossil and many extant taxa never have been included in phylogenetic analyses up to now. Nevertheless, the number of phylogenetic trees and the available molecular data of neoselachians have increased in recent years significantly. The application of different data sets (morphology vs. genetics) also occasionally has a fundamental impact on the composition of the clades as shown in a study on squaliform sharks (KRIWET & KLUG in press).

Dental characters of Neosleachii

Skeletal remains of fossil neoselachians are very scarce compared to the rich fossil record of isolated material, such as teeth, placoid scales or fin spines. Tooth morphologies and their ornamentations certainly have high taxonomic potential in

neoselachians, and are almost the only diagnostic aspect of most extinct taxa (e.g. LERICHE 1906; CASIER 1947a, b, c; ARAMBOURG 1952; HERMAN 1977). Whereas the tooth crown of neoselachians might taxonomically useful at generic and specific levels, the tooth root is useful for higher taxonomic levels. Especially the vascularisation pattern (pattern of the openings of nerves and blood vessels) of the tooth root is characteristic for the different neoselachian orders. However, ontogenetic and sexual dimorphism variability of neoselachian dental morphologies is poorly known (e.g. BASS *et al.* 1973; GRUBER & COMPAGNO 1981; SÁEZ & LAMILLA 1997, 2004; STRAUBE *et al.* 2008). Only the combination of extant and fossil taxa – isolated teeth as well as skeletal remains – enables to establish useful characters including tooth features that are useful for taxonomic and systematic purposes. Nevertheless, the early evolution and diversification of neoselachians only could be reconstructed if the vast number of taxa only known by teeth also is considered.

Remarks on synechodontiform monophyly

DUFFIN & WARD (1993) erected for the first time the clade Synechodontiformes including the families Orthacodontidae and Palaeospinacidae. They identified this group as belonging to the neoselachian clade Squalomorphii. However, closer relationships of synechodontiforms to galeomorph sharks were repeatedly assumed by various scientists based predominantly on dental but also on a few skeletal characters (e.g. WOODWARD 1889; CAPPETTA 1973, 1987, 1992; HERMAN 1977; MAISEY 1985; BÖTTCHER & DUFFIN 2000; CUNY *et al.* 2001; KRIVET & KLUG 2004). In addition to the controversy about the systematic position of this clade within Neoselachii, the monophyly of this clade was debated mainly in the last decades.

The monophyly of Synechodontiformes is predominantly based not on skeletal but on characteristic dental features including the vascularisation pattern of the tooth roots. Contrary to the hypothesis of a monophyletic grouping Synechodontiformes, MAISEY *et al.* (2004) stated that the four synechodontiform taxa *Sphenodus*, *Paraorthacodus*, *Synechodus* and “*Palaeospinax*” represent an “assortment of different stem neoselachians and / or galeomorphs”, because of the incongruent distribution of the pseudopolyaulacorhize vascularisation root pattern, which they consider not to be developed in *Sphenodus* (contrary to BÖTTCHER & DUFFIN 2000). Moreover, BÖTTCHER & DUFFIN (2000) reconstructed the dentition of the orthacodontid shark *Sphenodus macer* (QUENSTEDT, 1851) as having a single row of upper intermediate teeth, which is a characteristic feature of lamniform sharks (Lamniformes, Galeomorphii; COMPAGNO 1984; SHIMADA 2001, 2002). Consequently, MAISEY *et al.* (2004) argue that *Sphenodus* might be more probably a member of lamniforms

based on the presence of intermediate upper teeth, absence of distinct pseudo-polyaulacorhize root pattern and tooth crown morphology. However, tooth crown morphology is a problematic character, because it strongly depends on feeding adaptations and similar tooth morphologies are convergently developed in different neoselachian lineages. A re-examination of the root of *Sphenodus* (and other supposedly basal synechodontiforms such as *Rhomphaiodon* DUFFIN, 1993b and *Welcommia* CAPPETTA, 1990) by me shows, conversely to the statement by MAISEY *et al.* (2004) that it displays the typical synechodontiform vascularisation pattern of the root with distinct labial root depression to which basally open nutritive grooves are restricted (see also chapter “Results”).

Although there is a wide array of controversies concerning the monophyly and systematic position of Synechodontiformes within Neoselachii, the different hypotheses have never been tested using robust cladistic principles including all taxa assigned to this group up to now. The foremost difficulty including all taxa into a comprehensive phylogeny of Neoselachii is founded on the scarcity of skeletal material. A revision of articulated specimens of fossil sharks and rays enabled the discovery of several skeletons of palaeospinacid genera from Jurassic strata (e.g. KRIWET & KLUG 2004 and herein).

Remarks on palaeospinacid taxonomy

Within Synechodontiformes the family Palaeospinacidae is considered the most diverse group with more than 30 species, which are almost exclusively known by isolated teeth. In 1843, L. AGASSIZ described a single vertebral column and shagreen of placoid scales from the Early Jurassic of Lyme Regis (South England), which he referred to the genus *Thyellina* MÜNSTER in AGGASIZ (1843) according to the similarity to *T. angusta* (= *Scylliorhinus angustus*) from the Campanian of north-western Germany. Due to the lack of any useful characters but because of the different age he erected the new species *T. prisca* simultaneously indicating that it might represent a new genus. In 1872, EGERTON described a few incomplete skeletons from the same locality where L. AGASSIZ' specimen was found and which were acquired by Lord ENNISKILLEN (UK), suggesting that these specimens and the holotype of *T. prisca* “could not belong to the genus *Thyellina*, which has no dorsal fin spines, nor to the family Scylliadae (cat sharks [annotation by the author]), but ought to be removed to the family Spinacidae (including the dogfish sharks [annotation by the author]). He concluded, as L. AGASSIZ already indicated, that these specimens represent a different, hitherto unknown genus, more closely related to the genus *Acanthius* (= *Hetero-*

dontus) than to any other extant or fossil shark taxon. Accordingly, EGERTON (1872) erected the new taxon, *Palaeospinax*. In addition, he mentioned a single specimen from the Liassic of south-western Germany, “which much resemble those of *Palaeospinax*, but the materials are too imperfect to justify such as classification”. In 1889, A. S. WOODWARD designated the German specimen as the holotype of *Palaeospinax egertoni*. In the following years, several new specimens were assigned to *P. priscus* (EGERTON 1873; DAVIS 1881; FRAAS 1896; JAEKEL 1898; DEAN 1909; MAISEY 1977). In 1932, A. S. WOODWARD stated that the taxon *Aulakisanthus*, erected by TERQUEM & PIETTE (1865) is a junior synonym of *Palaeospinax*.

In 1863, F. J. MACKIE established a new species “*Hybodus dubrisiensis* from the Cretaceous of England based on several skeletal remains, which was transferred to a new genus, *Synechodus*, by WOODWARD (1888). In the following, most Jurassic synechodontiforms were referred to *Palaeospinax*, whereas Cretaceous and Palaeogene taxa were included in *Synechodus*. Nevertheless, distinguishing *Palaeospinax* from *Synechodus* remained a major reason for controversial discussions over decades to follow.

WOODWARD (1888: 325) already indicated that *Synechodus* is “so far as is known, scarcely differing from *Palaeospinax*”. Almost hundred years later, CAPPETTA (1987: 130) stated that the tooth morphology of *Synechodus* is very similar to *Palaeospinax* so that “it is not impossible that the two genera are synonymous”. Except for unconvincingly dental characters, the only significant distinguishing character is the presence of dorsal fin spines in *Palaeospinax* and the lack of those in *Synechodus*. However, all *Synechodus* material from the Chalk of England is too fragmentary to compellingly conclude if there were dorsal fin spines or not. Dorsal fin spines are present in living sharks in different groups, but are not taxonomically useful according to loss of fin spines convergently several times in the evolution of neoselachians (HUBBS & MCHUGH 1951; COMPAGNO 1984).

Although a few *Palaeospinax* specimens display well-preserved dentitions in addition to anterior parts of the skeleton, the description of tooth morphologies in this taxon remained indistinctive for long (see chapter “Results”). However, the articulated dentitions of *Synechodus* are well-figured and described by MACKIE (1863) and WOODWARD (1886, 1888, 1891). This might be the main reason, why new species were assigned to this genus rather than to *Palaeospinax* (e.g. LERICHE 1911; AMEGHINO 1935; CASIER 1943). With the intention to establish useful dental characters, GLIKMAN (1957) was able to discover dental differences between *Synechodus dubrisiensis* and *Synechodus recurvus* TRAUTSCHOLD, 1877 and subsequently introduced the new genus *Paraorthacodus* for the latter. With the exception of the

species assigned to *Palaeospinax* and *S. dubrisiensis*, all palaeospinacid species known to date are based on isolated teeth.

CAPPETTA (1973) in trying to resolve the controversies and developing a useful taxonomic framework suggested to establish two groups. The first one includes taxa displaying teeth with an overhanging labial crown base over the crown-root junction and broadly united lateral cusplets. The second group shows no overhanging crown base and has well-separated lateral cusplets. HERMAN (1974) followed this scheme and suggested to unite *S. nitidus*, *S. lerichei*, *S. dubrisiensis* and *S. hesbayensis* in the first group, and *S. recurvus* and *S. nerviensis* in the second. However, he didn't apply different names to the two groups but maintained the name *Synechodus* for all. THIES (1991) suggested lumping all palaeospinacid teeth together in *Palaeospinax* because no sufficient dental difference between the genera could be established for differentiation on supra-specific level. He concluded that tooth morphologies may be symplesiomorphies or products of convergent evolution. CAPPETTA (1992) contradicted this interpretation vehemently and argued for separating *Synechodus* and *Palaeospinax* on the basis of stronger labial striae and decreasing overhanging of the labial crown base in *Palaeospinax*. THIES (1992, 1993) continued to disagree and this dispute was not resolved according to unavailable useful and applicable dental characters for all species.

This dispute triggered DUFFIN & WARD (1993) to revise the skeletal material of *Palaeospinax* from the Lower Jurassic of Lyme Regis and trying to present several valuable dental characters to settle the controversies. They concluded that the holotype of *Palaeospinax priscus* – a single vertebral column without other skeletal elements – lacks any diagnostic characters to define the genus *Palaeospinax*. Consequently, they considered *Palaeospinax* to be a *nomen dubium*. DUFFIN & WARD (1993) determined that *Palaeospinax* and *Synechodus* display a very similar morphology and consequently all species formerly assigned to *Palaeospinax* were transferred to *Synechodus*. Although they presented several valuable dental characters distinguishing *Synechodus* and *Paraorthacodus*, the taxonomic scheme still remained difficult. One problem is the presence of fin spines in the Lower Jurassic specimens and the absence of fin spines in all other species of *Synechodus* as far as known (see also chapter "Results and Conclusions") Additionally, the problems to differentiate *Synechodus* and *Paraorthacodus* and to assign the different species without doubt to any of the two genera remained largely unresolved according to the scarcity of skeletal remains. The revision of the neoselachian fauna of the Upper Jurassic lithographic limestones of southern Germany by KRIWET & KLUG (2004) revealed several undescribed and deceptively assigned skeletal remains. Thorough

comparison of these Late Jurassic neoselachian taxa enabled them to classify several small neoselachians as members of *Paraorthacodus* and *Synechodus*, which represent the first skeletal remains of this group from the Late Jurassic at all up to now. These palaeospinacid specimens allowed me to overcome the problems in identifying useful taxonomic characters and to perform a detailed cladistic analysis of the interrelationships of all members of Synechodontiformes (see chapter “Results and Conclusions”).

Material and Methods

For this doctoral dissertation different data sets of fossil synechodontiform sharks were investigated and analysed. In addition to the large amount of available literature about synechodontiform records, accessible skeletal and dental materials were examined. Altogether, skeletal remains constituted the main scope of this project. Described, but also undescribed or wrongly assigned skeletal material of different collections all over Europe and North America was studied. Conservation lagerstätten yielding synechodontiform remains are the Lower Jurassic of Lyme Regis (South England) and Holzmaden (Southwest Germany), the Upper Jurassic Lithographic Limestones of the Solnhofen area (Southeast Germany), Nusplingen (Southwest Germany) and Cerin (Southeast France), and the Upper Cretaceous Chalk of England. All other conservation lagerstätten, for example the Late Cretaceous localities of Lebanon or the Niobrara Limestone of the U.S.A., didn't yield any synechodontiform remains up to now. In addition to the material present in different collections, new findings of mainly palaeospinacid skeletons were excavated during new field campaigns of the Staatliches Naturkundemuseum Stuttgart (SMNS). Photographs of skeletal remains were predominantly taken under normal light using in special cases ultraviolet light to emphasize informative soft-part structures. Drawings were performed with a Zeiss stereomicroscope equipped with a camera lucida.

For many decades studying skeletal material caused major problems in that the dentitions and teeth are generally still embedded in the matrix and barely accessible. Extracting teeth from articulated fossils for study with a Scanning Electronic Microscope (SEM) generally result in severely damaging the specimen and/or destroying the very small and delicate teeth. Impeding the destruction of the scarce specimens a new method to obtain high-quality casts was developed during this doctoral thesis by the author. Small forms for casts of the embedded teeth were prepared using very precise silicon compound, which dries very slowly avoiding bubbles to be developed. Subsequently the silicon forms were filled with low viscos-

ity and also slow siccative epoxy resin. This resulted in the creation of high-resolution casts that are indistinguishable from the original teeth displaying also the most delicate structures. These casts were studied using a SEM and photographs were gathered for documentation.

In addition to skeletal remains, all available isolated material, such as teeth, placoid scales and fin spines, were examined in different collections all over Europe and North America. Furthermore a field campaign to the Upper Jurassic deposits of north-eastern Spain was conducted in 2006. The generated samples of 650 kg of marls from different localities in the Iberian Basin were prepared with hydrogen peroxide and acetic acid, screen washed, and finally sorted under a microscope for vertebrate remains. This material was also examined for comparison in this study as well as thousands of neoselachian teeth of the Upper Jurassic locality of Mahlstetten (SW Germany), which were collected and provided by Elmar Unger (Aulendorf, Germany). SEM photographs of isolated material were taken at the Ludwig-Maximilians-University of Munich and the Museum für Naturkunde Berlin. Phylogentic methods used in this doctoral thesis are described in detail in **Paper 7**, whereas the applied methods of the diversity analyses are also exhaustive explained in **Paper 8** and **9**.

Institutional Abbreviations: **AMNH**, American Museum of Natural History, New York, U.S.A.; **BMM**, Bürgermeister-Müller-Museum, Solnhofen, Germany; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **GPIT**, Geologisch-Paläontologisches Institut, Universität Tübingen, Germany; **JME**, Jura-Museum Eichstätt, Germany; **LMU**, Ludwig-Maximilians-University, Munich, Germany; **M-Bergér**, Museum Bergér, Harthof (Eichstätt), Germany; **MfN**, Museum für Naturkunde Berlin, Germany; **NHML**, National History Museum London, United Kingdom; **RBINS**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **SMF**, Senckenberg-Museum Frankfurt, Germany; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Germany; **TFB**, Tierpark and Fossilium Bochum, Germany.

Results and Conclusions

In an effort to reconstruct the phylogeny and evolution of an extinct group of sharks commonly called the Synechodontiformes and to identify their position within cartilaginous fishes and their relations to modern sharks, rays and skates, the Neoselachii, a detailed study of skeletal remains and isolated teeth was carried out. Since this group is exclusively fossil without any extant representatives, the phylo-

genetic analyses are based on morphological characters only. Additionally, skates and rays, the Batoidea, were omitted from the analyses presented here because of their controversial position within neoselachians or as sister group to all sharks depending on the use of characters (morphology vs. molecular). In the following, the main results of this study are presented.

DUFFIN & WARD (1993) were the first to unite the Orthacodontidae AGASSIZ, 1843 and Palaeospinacidae REGAN, 1906 (= Synechodontidae CASIER, 1947a) in the order Synechodontiformes. Orthacodontidae were previously considered to be member of Hexanchiformes, whereas Palaeospinacidae (including *Nemacanthus*, *Palaeospinax*, *Paraorthacodus*, *Synechodus*) were left as *incertae sedis* within Galeomorphii (e.g. CAPPETTA 1987). HERMAN (1977) considered palaeospinacids to be closely related to hybodonts, which was, however, refuted by REIF (1977) based on the ultrastructure of the tooth enameloid and by MAISEY (1977) based on the structure of fin spines in *Palaeospinax*. The monophyly of Synechodontiformes predominantly was based not on skeletal but on characteristic dental features including the peculiar pseudopolyaulacorhize root vascularisation pattern by DUFFIN & WARD (1993) that was, however, not commonly accepted.

Until 2005, when this project started, the following genera within Synechodontiformes have been distinguished: *Breviacanthus* MAISEY, 1976 (Early – Middle Jurassic), *Mucrovenator* CUNY *et al.*, 2001 (Late Triassic – Early Jurassic), *Nemacanthus* AGGASIZ, 1843, *Palaeospinax* EGERTON, 1872 (Early Jurassic), *Paraorthacodus* GLIKMAN, 1957 (Late Jurassic – Palaeocene), *Pseudonotidanus* UNDERWOOD & WARD, 2004a (Late Triassic – Early Jurassic), *Rhomphaiodon* DUFFIN, 1993b (Middle Triassic – Early Jurassic), *Sphenodus* AGASSIZ, 1843 (Early Jurassic – Palaeocene), *Synechodus* WOODWARD, 1888 (Late Jurassic – Palaeocene) and *Welcommia* CAPPETTA, 1990 (Late Jurassic – Early Cretaceous).

For many decades, taxonomic controversies focused on the use of dental characters in this group. Subsequently, different concepts were proposed, which, however, never have been tested using cladistic principles including all taxa and specimens assigned to this group up to now. The foremost difficulty including all taxa in a comprehensive phylogeny of Neoselachii is because of the lack of useful skeletal material. In the course of this project, as many skeletal remains of fossil neoselachians from all over Europe, North America and Asia housed in numerous institutional and museum collections were re-evaluated and identified. This led to the discovery of abundant skeletal remains of different synechodontiforms previously not known or wrongly identified (e.g. KRIWET & KLUG 2004).

Successive taxonomic revisions of articulated skeletal remains from the Early

and Late Jurassic and of isolated teeth from different epochs enabled the identification of additional, hitherto unknown taxa with synechodontiform affinities, thus increasing the taxonomic diversity of this group. KLUG & KRIWET (2008) identified all Early Jurassic specimens assigned to *Palaeospinax* characterized by dorsal fin spines as a new genus, *Palidiplospinax* agreeing with DUFFIN & WARD (1993) that the holotype of the generotype is indeterminable (**Papers 1–2**). *Palidiplospinax* KLUG & KRIWET, 2008 is mainly known from the Early Jurassic of England (Lyme Regis) by numerous skeletons of *P. enniskilleni* and *P. occultidens* and the Early Jurassic of South-West Germany (Holzmaden) by a single skeletal remain of *P. egertoni*. A second species, *P. smithwoodwardi*, based also on a single specimen was described from Holzmaden by FRAAS (1896) consisting of an isolated vertebral column with appendages but lacking the skull. The validity of this species was established by KLUG & KRIWET 2006 (**Paper 2**). This specimen is remarkable in that it allowed a detailed description of the male clasper organs of an extinct shark for the first time.

Outside Lyme Regis and Holzmaden, isolated teeth belonging to *Palidiplospinax* were reported from the Early Jurassic of North Germany (THIES 1983) and North Italy (*P. pinnai* (DUFFIN, 1987)). LAMBE (1918) described a partial skeleton including the caudal and anal fins but lacking the skull from the Late Cretaceous of Alberta (Canada) as *Palaeospinax ejuncidus*. However, the specimen is too fragmentary to allow any identification. According to our current understanding, *Palidiplospinax* is restricted to the Early Jurassic. Isolated fin spines from the Late Triassic assigned to *Nemacanthus* and from the Early and Middle Jurassic named *Breviacanthus* were repeatedly included within Synechodontiformes in the past, generally with close affinities to *Palaeospinax*. However, CUNY (1998) combined the fin spines of *Nemacanthus* with teeth of *Rhomphaiodon* and the fin spines collectively called *Breviacanthus* belong to *Palidiplospinax*. From the Holzmaden deposits, the only skeletal remain of *Pseudonotidanus* (*P. politus*) is known (KLUG in prep.).

Even though a detailed revision of all species assigned to synechodontiform genera, especially those based on teeth, was beyond the scope of this project, some species from the Jurassic and Cretaceous were reconsidered. This resulted, i.e., in that a Middle Jurassic tooth taxon, *Synechodus prorogatus* KRIWET, 2003a, is now considered to represent a different taxon (REES & KLUG in prep.).

So far, the fossil record of synechodontiform sharks from the Late Jurassic of the famous lithographic limestones of the Solnhofen area (Bavaria, Germany) and Nusplingen (Baden-Württemberg, Germany) was very limited with two species of *Sphenodus* (*S. nitidus* from Bavaria and *S. macer* from Baden-Württemberg), a single species of *Paraorthacodus* (*P. jurensis* from Baden-Württemberg) and a single

tooth from Bavaria assigned to *Synechodus* without species assignment (LEIDNER & THIES, 1999). KRIWET & KLUG (2004) also indicated the presence of skeletal remains of *Synechodus* and *Paraorthacodus* in the lithographic limestones of Solnhofen but did not provide detailed descriptions or revisions. A subsequent analysis of these remains also enabled to identify the small Late Jurassic shark *Macrourogaleus*, which was originally assigned to Scyliorhinidae, also to belong to Synechodontiformes because of its characteristic dental pattern (**Paper 3**).

An incomplete and disarticulated skeleton of a small neoselachian shark and additional isolated teeth from the Kimmeridgian of Baden-Württemberg represent the first unquestionably record of *Synechodus* in the Upper Jurassic lithographic limestones of Germany. The skeleton includes parts of the vertebral column, the left palatoquadrate, the right Meckel's cartilage, several fragments of calcified cartilage of the cranial skeleton, 32 teeth, and several placoid scales. Additional isolated teeth of this species occur in the Kimmeridgian of Mahlstetten. These specimens were assigned to a new species, *S. ungeri* because of diagnostic dental traits (**Paper 4**).

The skeletal morphology of *Paraorthacodus jurensis* was re-described based on the incomplete holotype and a newly discovered almost complete specimen (**Paper 5**). The latter specimen allowed the detailed examination of the postcranial skeleton of *Paraorthacodus* for the first time. Most conspicuous is the presence of a single spine-less dorsal fin. In this respect, *Paraorthacodus* differs from most palaeospinacids known by skeletal remains, but resembles *Macrourogaleus*. The new specimen differs from the holotype in having one additional pair of cusplets in all tooth positions, which strongly supports sexual dimorphism in this species. However, an assignment to male or female is impossible, because the holotype lacks most parts of the postcranium and the new specimen is, unfortunately, poorly preserved in the pelvic region. Additionally, the re-evaluation of Late Jurassic skeletal remains of neoselachians yielded two other specimens of *Paraorthacodus* occurring in Tithonian of the Solnhofen area (KLUG in prep.; see also **Paper 1**). These specimens are assumed to be juveniles of *Paraorthacodus jurensis*, which is supported by morphometric measurements.

A single study on Southern Hemisphere synechodontiform sharks with special focus on Late Cretaceous Antarctic taxa (**Paper 6**) enlarged the knowledge of Gondwana synechodontiforms during the Cretaceous. A new species of *Paraorthacodus*, *P. antarcticus*, was introduced in this study. Teeth of *Sphenodus* (generally without species identification) were described from the Late Jurassic of Tanzania (ARRATIA *et al.* 2002), late Campanian of Angola (ANTUNES & CAPPETTA 2002), Campanian of Antarctica (RICHTER & WARD 1990; KLUG *et al.* 2008), and Maastrichtian of Antarctica

(GRANDE & EASTMAN 1986; GRANDE & CHATTERJEE 1987). The Campanian and Maastrichtian remains from Antarctica are the youngest Gondwanan records and represent the southern-most occurrences of *Sphenodus*.

In Gondwanan, *Synechodus* occurrences are comparably rare and are known from the Late Cretaceous of New Zealand (PFEIL 1983; KLUG *et al.* 2008) and Argentina (AMEGHINO 1893; ARRATIA & CIONE 1996). Gondwanan occurrences of *Paraorthacodus* were reported from the Upper Cretaceous of Australia (KEMP 1991; SIVERSON 1997), New Zealand (DAVIS 1888; CHAPMAN 1918; CAPPETTA 1987), Argentina (AMEGHINO 1893; ARRATIA & CIONE 1996), and Chile (ARRATIA & SCHULTZE 1999). The species *P. antarcticus* is the first record of this genus in Antarctica. In addition, KRIWET (2003b) described an unidentified palaeospinacid tooth from the Lower Cretaceous (Valanginian – Aptian) of Antarctica. The occurrence of synechodontiform sharks in the Cretaceous of Antarctica correlates with an interval of enlargement of the trans-equatorial Tethyan seaway within the Coniacian-Maastrichtian interval. The absence of all synechodontiforms in Antarctica after the K/T boundary, conversely, concurs with a drop in surface water temperatures.

However, up to now, the existence of the taxon Synechodontiformes still remains to be established. In the course of these taxonomic revisions, abundant dental and skeletal data of synechodontiform taxa were accumulated for a subsequent phylogenetic analysis employing robust cladistic principles (**Paper 7**). In doing so, several questions central to the existing controversies were addressed: (1) are Synechodontiformes monophyletic? (2) are Synechodontiformes member of Neoselachii? (3) and if so, what is their position within Neoselachii? and finally (4) what are the interrelationships of taxa assigned to Synechodontiformes if this group is monophyletic?

Morphological characters used in this study come from different sources. First, a character list was generated by combining anatomical characters used in three previous phylogenetic analyses of neoselachian interrelationships: (1) CARVALHO (1996), (2) CARVALHO & MAISEY (1996), and (3) SHIRAI (1996). The compiled character list was examined carefully to identify repeatedly and redundant characters, which were necessary corrected. Some characters with varying polarity coding by different authors were simplified and if applicable split (multistate characters) and coded as binary character states. Compiling character lists from published analyses and eliminating redundant characters resulted in the identification of 138 anatomical characters. Additionally, 36 new characters were added: seven cranial, 11 postcranial, 10 general dental, six tooth root, and two tooth crown characters.

The total combined data matrix comprised 174 characters. Although molecular

sequences are becoming increasingly abundant and accessible, they were not considered in these analyses because the group under consideration comprises exclusively extinct taxa without the possibility to perform molecular analyses. The focus of this study is to enhance morphological character sampling for neoselachian phylogenetics including extinct taxa, providing a comprehensive morphological database.

The phylogenetic relationships of either neoselachians as well as synechodontiform sharks were explored using cladistic principles (WILEY *et al.* 1991). Four different analyses were performed (**Paper 4**). The neoselachian analysis includes 174 (152 binary as well as 22 multistate) characters and 29 taxa in addition to the outgroup. The analysis of synechodontiform interrelationships comprises 35 binary characters and 11 taxa. As outgroup, the taxon *Hybodus* including three species (*H. hauffianus*, *H. fraasi*, *H. basanus*) was used.

The main results that can be derived from these phylogenetically analyses are (**Paper 7**):

- (1) all taxa assigned to Synechodontiformes so far (see above) form a monophyletic group, which is well-supported by morphological characters;
- (2) Synechodontiformes is the basal sister group to all living sharks;
- (3) the systematic concept of Neoselachii has to be expanded to include also extinct groups that are not nested phylogenetically within Neoselachii but display characteristic neoselachian features (e.g. calcified vertebral centra, etc.);
- (4) the interrelationships within Synechodontiformes remain largely unresolved due to the fact that several genera are known from isolated teeth only (“nov. gen.” *prorogatus*, *Mucrovenator*, pre-triassic “*Synechodus*”, *Rhomphaiodon*, *Welcommia*);
- (5) it is possible to identify four monophyletic groupings within Synechodontiformes, which are cladistically well-supported:
 - **Pseudonotidanidae**: [*Welcommia* + *Pseudonotidanus*]
 - **Orthacodontidae**: *Sphenodus*
 - **Palaeospinacidae**: [*Palidiplospinax* + [“nov. gen.” *prorogatus* + *Synechodus*]]
 - **Paraorthacodontidae nov. fam.**: [*Macrourogaleus* + *Paraorthacodus*];
- (6) the Middle Jurassic taxon “*Synechodus*” *prorogatus* KRIWET, 2003a represents a different genus, which is also present in the Late Jurassic (REES & KLUG in prep.);
- (7) the fossil record of Synechodontiformes ranges from the Late Permian to the Palaeocene supporting a Palaeozoic origin for Neoselachii;

(8) the reasons for their disappearance in the Palaeocene remain unclear.

Another, important result from the analyses here is that the Palaeospinacidae and Paraorthacodontidae together form the most diversified group of neoselachians during the Jurassic. With this new information at hand, it also was possible to reconsider the past diversity and biogeographic patterns of neoselachians (**Paper 8**). For this, the regional diversity and biogeographic patterns of European Late Jurassic neoselachians at genus level were analysed based on own samples and an extensive literature survey of about 40 localities ranging from the Oxfordian to Tithonian. This analysis used the simple completeness metric (SCM), which testifies a quite good fossil record of neoselachians in the Late Jurassic with a peak in the Kimmeridgian. Origination, extinction, diversification and turnover rates indicate that background origination occurred in the Oxfordian and Kimmeridgian with no disappearance of genera. In the Tithonian, background extinction is the main factor for neoselachian diversity decline. The decline in neoselachian diversity at the end of the Jurassic is most probably related to reduced habitats in the course of major regression events, establishment of physical barriers, and climatic changes. Faunal assemblages are quite uniform and mostly agree well with the contemporaneous palaeogeographic situation. The analyses indicate that both vicariance and dispersal were important processes in the biogeographic distribution of Late Jurassic neoselachians. This study, however, did not address the question of the timing of early diversification and radiation of modern sharks and batoids (Neoselachii) in Earth history.

There also exists a major controversy, which is related to discrepancies in taxonomic and phylogenetic interpretations favouring a Late Triassic or earliest Jurassic diversification and subsequent radiation event, respectively. For this, an analysis on Triassic and Jurassic neoselachians was carried out employing statistic procedures (**Paper 9**). In this study, sampling-standardization based on pooled taxonomic occurrences enabled to overcome the problem of a much richer neoselachian record in the Late Jurassic (monographic effect, because of lagerstätten) than earlier on. The standardized pattern of genus richness is one of low fairly constant diversity in the Late Triassic and earliest Jurassic with a steep rise in the Toarcian (ca. 180 Ma ago) representing the maximum diversification rate in the Jurassic towards a Middle and Late Jurassic plateau. The major Toarcian diversification agrees with conclusions based on phylogenetic analyses, but is in conflict to older interpretations based on raw data. Early Jurassic expansion of neoselachians was opportunistic in the aftermath of the end-Triassic mass extinction and the reasons for their rapid diversification and radiation probably include small body size, short life spans and oviparity enabling faster ecological reorganizations and innovations in body plans

for adapting to changing environmental conditions.

Final Remarks and Future Perspectives

The results derived from this study should prompt a critical re-evaluation of fossil elasmobranch systematics. Although the monophyly of Neoselachii is supported by both, molecular and morphological features, the extent to which extinct sharks should be included in Neoselachii remains a matter of debate. The analysis of an assortment of extinct sharks, which were considered either as belonging to different clades within neoselachians or distantly related elasmobranch groups, exemplifies the enormous potential of fossil taxa in phylogenetic analyses. However, care must be taken when morphological characters are used to infer phylogenetic relationships, which are simultaneously used in comparative analyses not to risk getting into circular argumentation. Molecular data, which might provide better estimates, cannot be used when the focus is on extinct taxa. The morphological data used here were thus all considered to be independent and were not used for anatomical arguments to avoid these circularities. The characters and taxon sampling carried out for this study represents the best and most inclusive estimate when morphology is considered. However, the phylogenetic analyses are characterized by rather high degrees of homoplasies. Homoplasies often are considered to represent “bad” data *per se* and much effort is sometimes undertaken to minimize the homoplastic distribution of characters by employing different methods. Interestingly, homoplastic character distribution seems to be common in phylogenetic analyses of elasmobranchs (e.g. CARVALHO 1996; CARVALHO & MAISEY 1996; SHIRAI 1996). Nevertheless, as long as these homoplastic characters display congruent distributions within a given tree, these characters still possess high potential for defining clades and sister groups. For this, careful character coding is crucial since the support for nodes is very sensitive to coding strategies. Therefore, all characters were coded as unordered with equal weights and, as already stated, independent from each other (**Paper 7**). The low resolution within Synechodontiformes is not the result of the rather high amount of homoplastic characters but more likely related to the restricted data set. Increasing the data set for providing better resolutions, however, require additional skeletal remains of taxa, of which only a limited number of teeth are available so far.

According to the results of this study, neoselachians were a minor element of past elasmobranch diversities over long periods during the Palaeozoic and the beginning of the Mesozoic. They experienced a first major radiation event at the end of the Early Jurassic, almost 73 million years after their first appearance in the

fossil record. The reasons for this are certainly related to small body sizes, short life spans and oviparity enabling faster ecological reorganizations and innovations in body plans for adapting to changing environmental conditions (**Paper 9**). However, biogeographic reasons (e.g. vicariance) or co-evolutionary patterns (interactions with hybodontoid or teleosts that also diversified rapidly during the Jurassic) cannot be ruled out completely. Phylogenetic analyses using more taxa of extinct chondrichthyans and enlarged data sets may provide better-resolved phylogenetic hypotheses and deeper insights into the factors triggering rapid diversification and radiation in the future.

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List of publications part for the thesis

- Paper 1 KLUG, S. & KRIWET, J. 2008. A new basal galeomorph shark (Synechodontiformes, Neoselachii) from the Early Jurassic of Europe. *Naturwissenschaften* 95: 443–448.
- Paper 2 KLUG, S. & KRIWET, J. 2006. Anatomy and systematics of the Early Jurassic neoselachian shark *Synechodus smithwoodwardi* (FRAAS, 1876) from southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2006(4): 193–211.
- Paper 3 KLUG, S. 2008. The Late Jurassic neoselachian *Macrourogaleus* FOWLER, 1947 is a palaeospinacid shark (Elasmobranchii; Synechodontiformes). *Acta Geologica Polonica* 58: 229–234.
- Paper 4 KLUG, S. in press. A new palaeospinacid shark (Chondrichthyes, Neoselachii) from the Upper Jurassic of southern Germany. *Journal of Vertebrate Paleontology*.
- Paper 5 KLUG, S., KRIWET, J., BÖTTCHER, R., SCHWEIGERT, G. & DIETL, G. in press. Skeletal anatomy of the extinct shark *Paraorthacodus jurensis* (Chondrichthyes; Palaeospinacidae), with comments on synechodontiform and palaeospinacid monophyly. *Zoological Journal of the Linnean Society*.
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- Paper 8 KRIWET, J. & KLUG, S. 2008. Diversity and biogeographic patterns of Late Jurassic neoselachians (Chondrichthyes, Elasmobranchii). In CAVIN, L., LONG-BOTTOM, A. & RICHTER, M. (eds): *Fishes and the Break-up of Pangaea*. Geological Society London, Special Publication 295: 55–69.
- Paper 9 KRIWET, J., KIESSLING, W. & KLUG, S. 2009. Diversification trajectories and evolutionary life-history traits in early sharks and batoids. *Proceedings of the Royal Society of London, Biological Series* 276: 945–951.

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