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Vertebrate fossils from the Kimmeridgian of Brunn: the oldest fauna from the Solnhofen Archipelago (Late Jurassic, Bavaria, Germany)

Oliver W. M. Rauhut^{1,2,3*}, Adriana López-Arbarello^{1,2,3}, Martin Röper^{4,1} & Monika Rothgaenger^{4,1}

¹SNSB, Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 Munich, Germany

²GeoBioCenter^{LMU}, Ludwig-Maximilians-University, Richard-Wagner-Str. 10, 80333 Munich, Germany

³Department of Earth and Environmental Sciences, Ludwig-Maximilians-University, Richard-Wagner-Str. 10, 80333 Munich, Germany

⁴Museum Solnhofen, Bahnhofstraße 8, 91807 Solnhofen

*Corresponding author; E-mail: o.rauhut@lrz.uni-muenchen.de

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Abstract

The locality of Brunn, Oberpfalz, represents the oldest setting within the area usually included within the Solnhofen Archipelago, dating to the Subeumela Subzone of the Late Kimmeridgian. The locality has yielded a rich vertebrate fauna from eight different levels of plattenkalks, dominated by actinopterygian osteichthyans. Apart from rare chondrichthyans, the fish fauna includes macroseiid gynlimodians, caturid and ophiopsid halecomorphs, as well as a new specimen of the enigmatic halecomorph *Ainia*, and a diverse array of teleosts. Tetrapods are represented by reptiles, including rare marine turtles, at least two new taxa of rhynchocephalians, an atoposaurid and a teleosaurid crocodyliform, and rhamphorhynchid and pterodactyloid pterosaurs. Whereas the fish fauna shows close affinities with other Kimmeridgian faunas, not only from the Solnhofen Archipelago, but also from other European sites, such as Cerin, a high degree of endemism is striking within the reptile fauna.

Key words: Solnhofen Archipelago, Kimmeridgian, Actinopterygii, Rhynchocephalia, Pterosauria

Zusammenfassung

Die Lokalität bei Brunn, Oberpfalz, ist in die Subeumela-Subzone des späten Kimmeridgium datiert und repräsentiert somit die älteste Fundstelle des Solnhofen-Archipels. Die Fundstelle hat eine reichhaltige, von Actinopterygiern dominierte Wirbeltierfauna aus acht verschiedenen Plattenkalkhorizonten geliefert. Abgesehen von seltenen Chondrichthyern beinhaltet die Fischfauna Gynlimodier der Familie der Macrosemiiden, Halecomorpha der Familien Caturidae und Ophiidae sowie ein neues Exemplar des seltenen Halecomorphen *Ainia* und eine diverse Teleosteer-Fauna. Tetrapoden sind durch Reptilien vertreten, darunter seltene marine Schildkröten, mindestens zwei neue Taxa von Rhynchocephalen, ein atoposaurider und ein teleosaurider Crocodyliforme und rhamphorhynchide und pterodactyloide Flugsaurier. Während die Fischfauna große Ähnlichkeit mit anderen Faunen des Kimmeridgiums, nicht nur des Solnhofen-Archipels, sondern auch anderer europäischer Fundstellen, wie etwa Cerin, weist die Reptilienfauna einen erstaunlich hohen Endemismus auf.

Schlüsselwörter: Solnhofen-Archipel, Kimmeridge, Actinopterygii, Rhynchocephalia, Pterosauria

1. Introduction

The Upper Jurassic limestones of southern Germany have long been known for their exceptionally preserved fossils (e.g. Barthel et al. 1990; Wellnhofer 2008; Arratia et al. 2015). Despite 200 years of collecting and research, new species are still being discovered frequently (e.g. López-Arbarello & Sferco 2011; Hone et al. 2012; Rauhut et al. 2012a, b; Schröder et al. 2012; Ebert et al. 2016), and even several new localities have been explored lately (e.g. Fürsich et al. 2007; Viohl & Zapp 2007; Ebert & Kölbl-Ebert, 2008; Heyng et al. 2011). What is less well

known, even in the technical scientific literature, is that the fauna that is collectively often called the “Solnhofen fauna” (or “fauna of the Solnhofen limestones”) actually includes components from different depositional settings and also different stratigraphic horizons (see e.g. Röper et al. 1996; Röper 2005). Indeed, fossils come from about a dozen different depocenters (the so-called “Wannen”; see Viohl 1985; Schmid et al. 2005) and span c. 3.5 Ma from the Late Kimmeridgian to the Early Tithonian (Schweigert 2007, 2015). The thin-bedded to laminated limestones of the southern Franconian Alb are thought to have been deposited in a number of depressions

within a sponge-algal-coral reef environment of an archipelago at the northern rim of the Tethys Ocean (Meyer & Schmidt-Kahler 1990; Keupp et al. 2007; Viohl 2015a), recently usually called the Solnhofen Archipelago. Tropical reef environments and archipelagos accumulate enormous proportions of global biodiversity because they evolve as a consequence of highly dynamic geological and climatic processes that generate and constantly modify barriers of dispersal. Thus, the Solnhofen Archipelago potentially housed a significant proportion of the Late Jurassic marine global biodiversity.

Although the Early Tithonian part of the Altmühl Formation in the Solnhofen – Eichstätt area (including the Eichstätt and Solnhofen members; see Niebuhr & Pürner 2014) is by far the most famous unit and has yielded most fossils so far, this mainly stems from the fact that these rocks have been exploited for commercial purposes for centuries, whereas the overlying Mörnsheim Formation and the underlying Torleite Formation (and equivalents) are as or even more fossiliferous, but have not been fully explored so far. The problem of the mixture of fossils from different depocenters and different stratigraphic intervals has been known for more than 100 years (Walther 1904; Mayr 1967), but only recently have attempts been made to distinguish the different faunas and see them in their stratigraphic, geographic and ecological framework (e.g. Röper 2005; Viohl & Zapp 2007; López-Arbarello & Schröder 2014; Ebert et al. 2015). Nevertheless, the generally excel-

lent knowledge of the geological and stratigraphic framework of these different localities (see Meyer 2015; Schweigert 2015; Viohl 2015a, b, c) provides a unique opportunity to study faunal evolution over a geologically short time in a regional setting. Indeed, the Solnhofen Archipelago represents a unique window into a Mesozoic shallow marine environment, in which we might be able to study the influence of local environmental differences and evolution over a short time scale (possibly speciation or species replacement) on faunal composition. An absolutely necessary prerequisite for such studies is a detailed understanding of the taxonomic composition of the faunas of the different localities / depocenters / stratigraphic levels concerned. Ongoing systematic studies have already shown cases of small clades comprising closely related species endemic to the Solnhofen Archipelago, the evolution of which seems to have been driven by palaeogeographical and chronostratigraphical changes (López-Arbarello & Schröder 2014; Konwert 2016).

The locality of Brunn (Oberpfalz) is one of the easternmost localities within the Solnhofen Archipelago (Textfig. 1). It was discovered as a fossil Lagerstätte in the early 1990ies and is protected as an important palaeontological site since 1993, following an official evaluation by one of the authors (M. Röper). It has been explored for fossils since 1993 by local enthusiasts (led by Monika Rothgaenger) in collaboration with Dr. Martin Röper of the Solnhofen Museum, and collected material is housed in the Bayerische

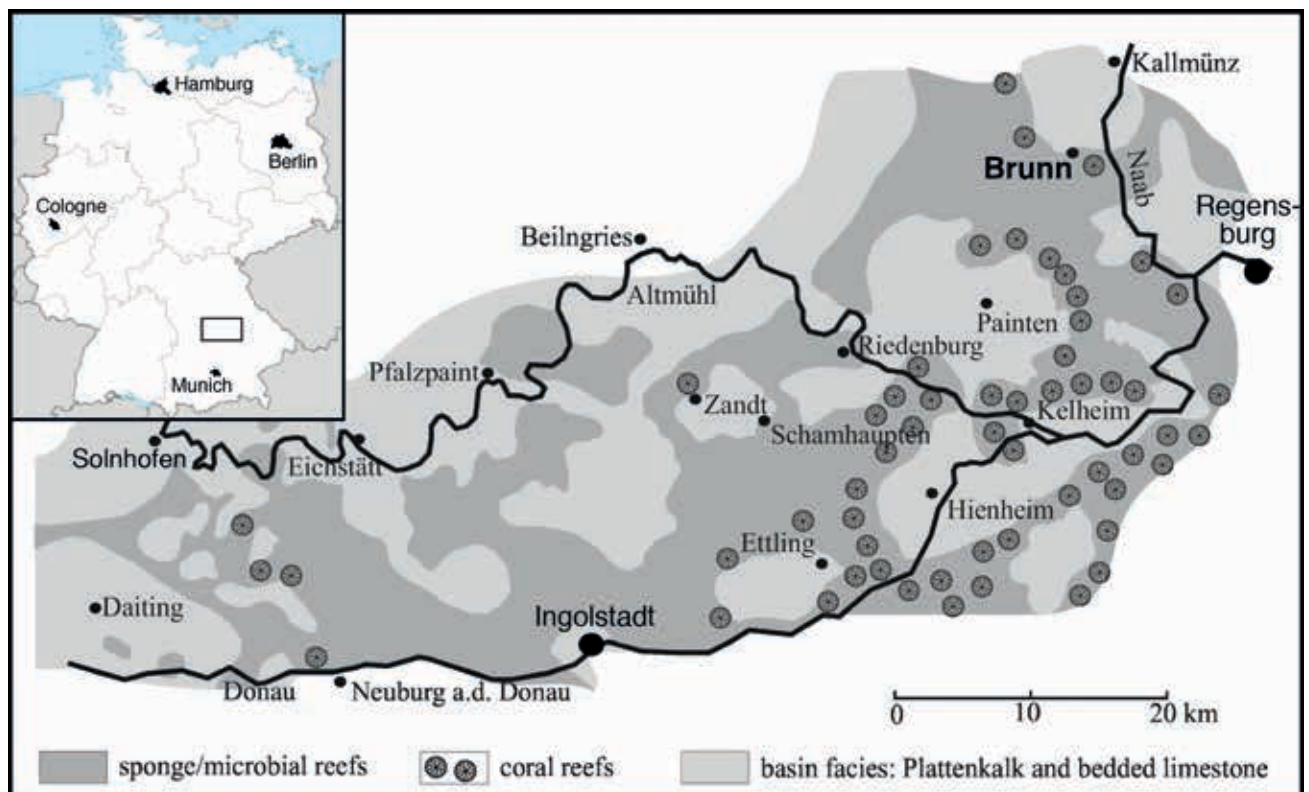


Figure 1: Map of the area between Solnhofen and Regensburg, with the palaeogeography of the Solnhofen Archipelago and the position of the locality Brunn indicated. Modified from Lane & Ebert (2015).

Staatssammlung für Paläontologie und Geologie in Munich (see Röper & Rothgaenger 1995; Röper et al. 1996; Röper 1997, 2005; Heyng et al. 2015). The locality of Brunn is especially noteworthy for representing the oldest fauna of the Solnhofen Archipelago, having been dated in the Subeumela Subzone of the Beckeri Ammonite Zone of the Late Kimmeridgian (Röper & Rothgaenger 1997; Schweigert 2007, 2015). The only older fossiliferous Plattenkalk locality in southern Germany, that of Wattendorf (Fürsich et al., 2007; Mäuser 2015), is some 100 km further to the north and might therefore not represent the same archipelago as the depocenters between Solnhofen and Regensburg. The locality of Brunn is thus of special interest for our understanding of the origin of the faunas of the Solnhofen Archipelago.

The limestones of Brunn are especially rich in plants and invertebrates, but a number of vertebrate specimens have also been found (Röper et al. 1996; Heyng et al. 2015). Only few of the fossils of Brunn have been scientifically analysed yet, and only two vertebrates have been described in detail so far. Arratia & Schultze (2013) described a new species of pachycormiform actinopterygian, *Orthocormus roeperi*, which is known from a single specimen. The other vertebrate published is the only complete pterosaur found, which was recently described as a new taxon of rhamphorhynchid, *Bellubrunnus rothgaengeri*, by Hone et al. (2012). An elasmobranch discovered in Brunn was furthermore identified as *Palaeoscyllium*, though not described in detail, by Thies & Leidner (2011). Likewise, a few actinopterygian specimens from Brunn were referred to previously known taxa: two specimens referred to *Ophiopsis* (= *Furo*) *muensteri* by Lane & Ebert (2012; see also Lane & Ebert 2015), and two specimens referred to *Macrosemius fourneti* by Ebert et al. (2016). Two rhynchocephalian specimens were briefly described in a popular science article by Rauhut & Röper (2013). However, none of these specimens has been described in detail.

The purpose of the present paper is to give an overview of the vertebrate fauna from Brunn, as far as it is known so far. Detailed descriptions and analyses of the respective taxa is beyond the scope of this work, but it will serve as a starting point for comparisons of the vertebrate fauna from this locality with that of other sites within the Solnhofen Archipelago.

2. Geological and palaeontological setting

As the geological and palaeontological setting of the locality of Brunn has been described in detail by Röper et al. (1996), Röper & Rothgaenger (1997), Röper (1997) and Heyng et al. (2015), only a brief overview will be given here. The locality of Brunn is the oldest and one of the easternmost and the most northern locality within the area that is usually included in the “Solnhofen Archipelago” (Textfig. 1). In the Late Jurassic, this area was part of the southern

Bavarian carbonate platform at the northern margin of the Tethys Ocean (Keupp et al. 2007). This platform was cut off by the Bohemian Massif in the east, but connected with further carbonate platforms that extended along the northern rim of the Tethys from eastern Bavaria to southeastern France (see Bernier & Gaillard 2015; Peyer & Khalloufi 2015). To the north, the shallow epicontinental sea that housed the south Bavarian carbonate platform was bordered by the Rhenian Massif. In the Late Jurassic, southern Germany was situated substantially further south than today, and thus presented a warm, semi-tropical setting, in which extensive sponge-microbial and coral reefs developed (Viohl 2015a). Due to sea-level changes, the Plattenkalk facies progressed from east to west from the Upper Kimmeridgian to the Tithonian (Viohl 2015a), with laminated limestones being deposited in shallow depressions (“Wannen”) between the reef complexes. The locality of Brunn is situated at the southern rim of one of the smallest of these depressions, the Pfraundorf-Heitzenhofener Basin. The section of the Brunn quarry exposes c. 8 m of sediments, presenting an intercalation of massive limestone layers and eight finely laminated Plattenkalk sections (Röper et al. 1996; Röper & Rothgaenger 1997; Heyng et al. 2015). Whereas the massive limestone layers are almost devoid of macrofossils, fossil remains were otherwise found throughout the section in the laminated limestones. The latter layers range from 10 to 80 cm in thickness and are often very finely laminated, with 1 cm of Plattenkalk including up to 70 distinct limestone laminae (Heyng et al. 2015). Water depth and/or hostile conditions apparently increased from the bottom to the top of the section, as the frequency of autochthonous benthic fauna and trace fossils decreases (Röper et al. 1996; Heyng et al. 2015). Finds of the index ammonite *Sutneria subeumela* in both the lower and upper part of the section constrain the age of the entire locality to the Subeumela Subzone of the Upper Kimmeridgian (Röper & Rothgaenger 1997; Schweigert 2007; Heyng et al. 2015). The fossil assemblage from Brunn is diverse and especially noteworthy for its high percentage of plants, which account for up to 25% of the macrofossils found (Heyng et al. 2015). Apart from aquatic dasycladalean green algae, the abundance of land plants is noteworthy, as it indicates a significantly higher terrestrial input than in most other Plattenkalk localities of the Solnhofen Archipelago. The invertebrate fauna includes most of the clades to be expected in a marine Jurassic setting, including brachiopods, gastropods, bivalves, cephalopods, crustaceans and diverse remains of echinoderms, although the planktonic crinoid *Saccocoma*, which represents one of the most common fossils found in the earliest Tithonian lithographic limestones of the Solnhofen-Eichstätt area, has not been identified so far (Röper et al. 1996; Röper 1997; Heyng et al. 2015). Vertebrate fossils are found throughout the section in basically all Plattenkalk in-

tercalations, but the preservation and completeness of specimens varies between different layers. Thus, the excellently preserved pterosaur *Bellubrunnus* was derived from Plattenkalk layer 6 (Hone et al. 2012), whereas layer 1 yielded an isolated pterosaur humerus (Röper 1997). Likewise, whereas fishes from layer 1 are often disarticulated (see Röper et al. 1996; Röper 1997), the upper layers have yielded some perfectly articulated fish specimens. On the other hand, the almost perfectly articulated rhynchocephalians were derived from Plattenkalk layer 2 (Rauhut & Röper 2013).

Institutional abbreviations: JME, Jura-Museum Eichstätt, Germany; MHNL, Museum d'Histoire Naturelle de Lyon, France; SNSB-BSPG, Staatliche naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

3. The vertebrate fauna

As it is to be expected in a marine setting, actinopterygian fishes represent the vast majority of the vertebrate specimens recovered from Brunn. Only few remains of chondrichthyans have been found so far. Tetrapods are represented by aquatic turtles, rhynchocephalians, two crocodylomorph remains, and a few pterosaur specimens.

3.1 Chondrichthyes

Only few chondrichthyan remains have been found so far (Heyng et al. 2015). Among them, one complete specimen (Textfig. 2) from plattenkalk layer 7 was identified as *Palaeoscyllium* ? sp. by Thies & Leidner (2011: 78), who also commented briefly on the morphology of its dermal denticles, but has yet to be described in detail.

3.2 Actinopterygii

More than a hundred actinopterygian specimens have been found in the excavations in Brunn only during the past twenty years. The preservation of the specimens is variable and ranges from excellently preserved, articulated skeletons to isolated body parts. More than half of the specimens could be identified to at least the generic level, but some 40 specimens were too fragmentary and could, at best, only be referred to higher taxonomic categories. Identification at the species level was often difficult, also due to the unresolved species taxonomy of many fish genera known from the Late Jurassic of southern Germany, so the following overview of the results mainly refers to genera. A more detailed analysis of the fish fauna of Brunn is currently under preparation by one of the authors (ALA) and co-workers.

Except for 28 species of acipenseriforms (sturgeons and paddlefishes), all other living actinopterygian taxa (more than 32,500 species according to the most recent counts by Eschmeyer & Fong [2016]) belong to a single clade called Neopterygii. Two main lineages are currently recognized within this clade: Teleostei, encompassing most of these species, and Holostei, which is currently represented by only seven species of gars (Ginglymodi: Lepisosteiformes) and the bowfin, *Amia calva* (Halecomorphi: Amiiformes). This tremendous asymmetry in the amount of living representatives of the main neopterygian lineages today does by far not reflect the situation during the early Mesozoic. During the Triassic-Jurassic the diversity of holosteans probably equaled or even exceeded that of teleosts. Both Teleostei and Holostei, including the two main holostean lineages Ginglymodi and Halecomorphi, are well represented in the plattenkalks of Brunn.



Figure 2: Elasmobranch *Palaeoscyllium* sp. from Brunn. Scale bar is in 1 cm increments.

3.2.1 Holostei: Ginglymodi

Two main lineages of Ginglymodi are currently recognized: Lepisosteiformes and Semionotiformes (López-Arbarello 2012; López-Arbarello & Wencker 2016). Only one lepisosteiform genus, *Scheenstia* López-Arbarello & Sferco, 2011 (including at least six species; López-Arbarello 2012) is represented with two species in the Solnhofen Archipelago (Schamhaupten, Kelheim, Eichstätt and Langenaltheim), but secure records of lepisosteiforms have not been found in Brunn so far. Röper (1997: 210) mentioned fragments of *Lepidotes* from plattenkalk layer 7, but we have not seen this material and the presence of Lepisosteiformes has thus yet to be confirmed.

Conversely, semionotiforms are much better represented in the Solnhofen Archipelago. With the exception of a few Middle Triassic species of still uncertain affinities, semionotiforms are classified in three families: Semionotidae, including freshwater species from the Late Triassic and Early Jurassic of Europe, South Africa and North America, and Callipurbeckiidae and Macrosemiidae, both including a very interesting diversity of marine taxa, ranging from the Middle Triassic to the middle Cretaceous of Europe, Africa and North America. The evolution of these two families seems to be directly related to the development of the Tethys and the opening of the Atlantic ocean. Both callipurbeckiids and macrosemiids are well represented and diverse in most of the Solnhofen basins, but only two macrosemiid genera have been found in Brunn so far: *Notagodus* and *Macrosemius* (Textfig. 3).

One of the macrosemiids found in Brunn is the genus *Notagodus*, with two complete specimens: a juvenile SNSB-BSPG 1993 XVIII P1, and a completely ossified, probably adult specimen SNSB-BSPG 1993 XVIII P2 (Textfig. 3A). Although a detailed study is necessary to properly identify these fishes, the largest specimen agrees in body proportions with the species *N. inimontis* according to Bartram (1977).

Macrosemius is represented by two complete and very well-preserved specimens (SNSB-BSPG 1993 XVIII VFKO-B 23 and VFKO-B 27; Textfig. 3B), which

were referred to *M.ourneti* by Ebert et al. (2016) in the most recent revision of this genus. The taxonomy of *Macrosemius* species is mainly based on meristic features (e.g., number of dorsal fin rays, number of dichotomizing vertical scale rows between dorsal fin and lateral line), but *M.ourneti* is further characterized by the series of enormous scutes protecting the caudal peduncle ventrally, between the anal and caudal fins, which are particularly well preserved in SNSB-BSPG 1993 XVIII VFKO-B 27 (Textfig. 3B).

3.2.2 Holostei: Halecomorphi

As mentioned above, there is a single living halecomorph species today, *Amia calva* (bowfin) which is restricted to North American freshwaters. Halecomorphs however, are broadly distributed in both freshwater and marine environments from the early Early Triassic to Recent. Halecomorphs are classified in two orders: the direct lineage to *Amia* is the Amiiformes and its sister lineage is the Ionoscopiformes (Grande & Bemis 1998). Both amiiforms and ionoscopiforms are present in Brunn.

Although the two amiiform families Amiidae, with two genera *Amiopsis* and *Solnhofenamia*, and Caturidae, with three genera, *Caturus*, *Amblysemius* and *Liodesmus*, are represented in different basins of the Solnhofen Archipelago, amiids have not yet been recorded in Brunn so far. In contrast, Brunn amiiforms include relatively large and complete caturid specimens. Among them, SNSB-BSPG 1993 XVIII VFKO-B 30 is very poorly preserved and it has not yet been possible to identify it at the generic level. Two other specimens, SNSB-BSPG 1993 XVIII P3 and SNSB-BSPG 1993 XVIII P4, which are complete and excellently preserved, most probably represent a new species of *Caturus* (Textfig. 4A). The specimen SNSB-BSPG 1993 XVIII P5 (Textfig. 4B) with a standard length (SL) of c. 45 cm represents a new and extraordinary large species of *Amblysemius* (other species in this genus reach up to c. 30 cm SL; Lambers 1994).

Ionoscopiform specimens from Brunn were referred to the Kimmeridgian species *Ophiopsis muen-*

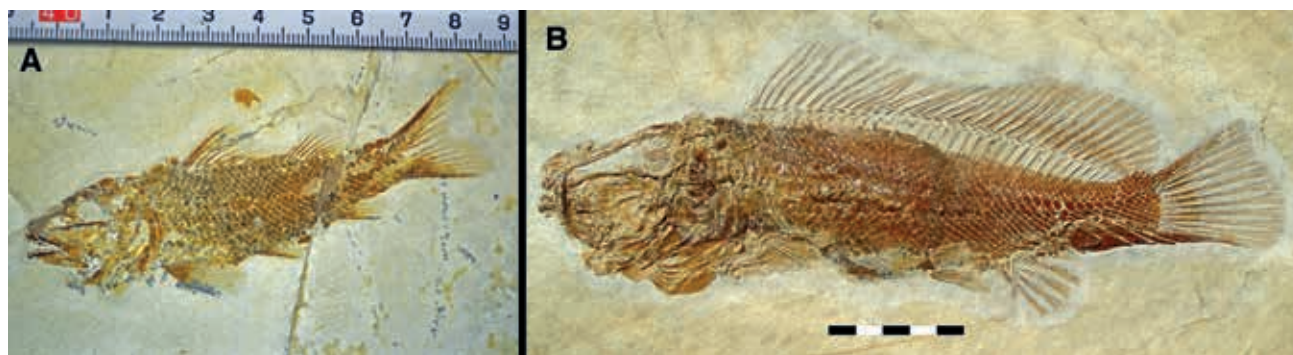


Figure 3: Macrosemiid Gynglymodii from Brunn. **(A)** *Notagodus* sp., SNSB-BSPG 1993 XVIII P2. **(B)** *Macrosemiusourneti*, SNSB-BSPG 1993 VIII VFKO-B 27. Scale bars are in 1 cm increments.

steri (Textfig. 4C) by Lane & Ebert (2012). This species is more widely known under the generic name *Furo* Gistel, 1848 and the generic name *Ophiopsis* Agassiz, 1834, is normally associated with other species (e.g. *O. procera*, *O. attenuata*). The nomenclature of these taxa was recently revised by Lane & Ebert (2015), who fixed the name *Ophiopsis* on the species *Ophiopsis muensteri* Agassiz, 1834, and created the new name *Ophiopsiella* for the species *Ophiopsis procera* Agassiz, 1843, and other closely related species. To our current knowledge the genus *Ophiopsiella* includes at least seven European and one African species, ranging from the Middle Triassic to the Early Cretaceous (Lane & Ebert 2015). According to Lane & Ebert (2012) the species *Furo orthostomus* Agassiz, 1841, *Furo normandica* Wenz, 1967, and *Ophiopsis muensteri* Agassiz, 1834 are likely to be congeneric under the name *Ophiopsis*. Several nominal species of *Furo* from the Tithonian localities of Bavaria are currently under study and might represent additional genera (Martin Ebert pers. comm. 2016).

One of the most amazing fossils found in Brunn is certainly SNSB-BSPG 1993 XVIII P6 (Textfig. 4D). Although the bones in the skull are crushed and thus broken, the whole fish is almost perfectly articulated and extraordinarily well-preserved. The fossil is clearly a specimen of *Ainia armata* (Wagner, 1846), which is a rare fish in the Late Jurassic limestones of Europe. The species is so far known from only several specimens from Cerin (MHNL 15260, MHNL 15389, MHNL 15469, MHNL 150724, MHNL 20271911, MHNL K203, MHNL K369, MHNL K724, MHNL K823), France, and two specimens from Germany: the holotype (BSPG AS-I-509) from Kelheim (Moser et al. 2017) and the new specimen from Brunn. Other specimens, such as SNSB-BSPG 1959 I 427 figured by Grande & Bemis (1998: fig. 422B), represent other species. The species has long been known under the name of *Callopterus agassizi* Thiollière, 1858, which was given to the French material (Saint-Seine, 1949, Lambers 1992). However, the generic name *Callopterus* Thiollière, 1858, is a nomen nudum (Nomenclator Zoologicus Volume 1: 543) and it was replaced by *Ainia* Jordan, 1919. On the other hand, Thiollière (1858: 784) and Saint-Seine (1949) listed *Lepidotus armatus* Wagner, 1846, as a junior synonym of *Callopterus agassizi* Thiollière, 1858. However, according to the ICZN Wagner's species name has priority. Therefore, considering all nomenclatorial rules and changes, the correct name of the species is *Ainia armata* (Wagner, 1846).

The new specimen from Brunn (SNSB-BSPG 1993 XVIII P7) shows very nicely the most distinctive feature of this species, which is the very incomplete squamation, limited to the dorsum and ventrum of the caudal peduncle. The scales are very small, quadrangular to circular and covered with a thick layer of ganoine. These scales are not organized in oblique rows oriented in anterodorsal to posteroventral direction like the normal body scales of other

actinopterygians. The scales of *Ainia armata* are also arranged in oblique rows, but these rows are oriented in posterodorsal to anteroventral direction in the dorsum and in posteroventral to anterodorsal direction in the ventrum of the caudal peduncle. This very peculiar kind of squamation is unique to *Ainia armata* among actinopterygians. SNSB-BSPG 1993 XVIII P6 is by far the most complete and best preserved specimen of this very rare species, making a detailed study of this enigmatic taxon possible (López-Arbarelo in prep.).

3.2.3 Teleostei

With 32639 valid living species (Eschmeyer & Fong 2016) Teleostei is the largest vertebrate clade. Although the monophyly of extant teleosts and their close phylogenetic relationships to several fossil taxa is generally well established and widely accepted, the delimitation of Teleostei has been problematic (see discussions in De Pinna 1996, Sferco et al. 2015). Following the long tradition of essentialist thinking in taxonomy (De Queiroz 1994), many authors attempted to delimit Teleostei on the basis of shared derived traits (e.g. Gosline 1965, Patterson 1973, 1977, Patterson and Rosen 1977, Gardiner et al. 1996, Arratia 1999, 2013). The disadvantages of apomorphy-based definitions have been extensively discussed (e.g. De Queiroz & Gauthier 1990, De Queiroz 1994) and recently De Queiroz (2013) stressed the feasibility of using a stem-based (branch-based, maximum clade) definition to define the name of a total clade. Apomorphy-based definitions of Teleostei depend on the features of the taxa that are added or excluded from the base of the clade [e.g. compare Arratia (1999: 323) with Arratia (2013: 115)] and arbitrarily apply the name Teleostei to one or another node along the stem to the crown-group.

In the same line of thought as De Queiroz (1994), De Pinna (1996: 150) proposed a clear and stable stem-based definition of Teleostei as follows: "Teleostei is here defined ... as the largest (i.e. most inclusive) actinopterygian clade not including either the Halecomorphi (*Amia* and close relatives) and/or the Ginglymodi (*Lepisosteus* and close relatives)". This total group definition equals the definition applied by Patterson (1977) and it is conceptually sound and stable. De Pinna (1996) further named the clade including all living teleosts and its fossil representatives as Teleocephala, and this node-based definition is stable and independent of our knowledge of a species representing the immediate sister taxon of the crown clade Teleostei (De Queiroz 2013).

For the reasons explained above, we accept the node-based clade Teleocephala and the stem-based clade Teleostei of De Pinna (1996). Accordingly, and accepting that they are more closely related to Teleocephala than they are to holosteans (Gardiner et al. 1996, Nursall 1996, Friedman et al. 2010, Arratia 2013, Sferco et al. 2015), pycnodontiforms, pa-

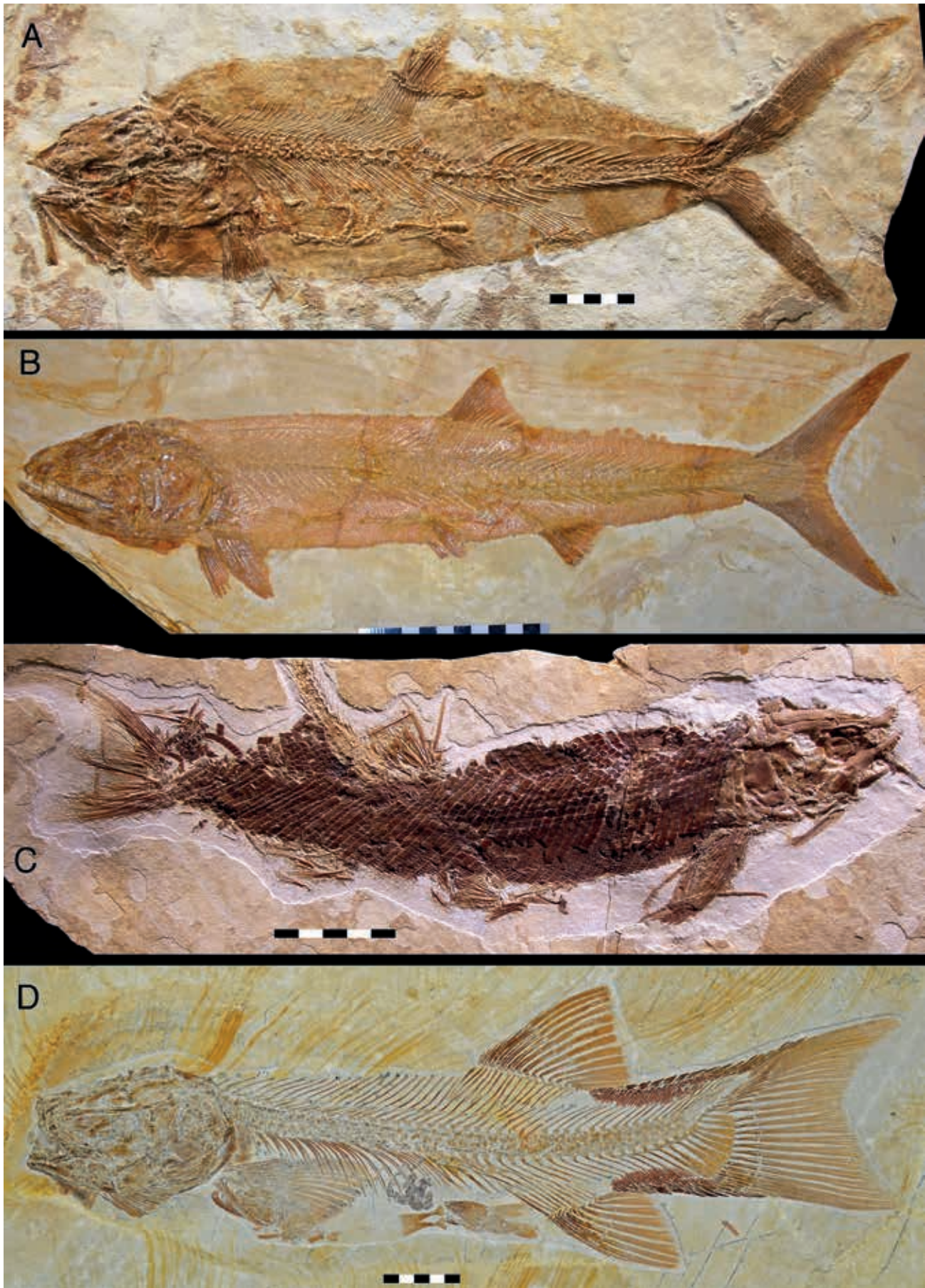


Figure 4: Halecomorphs from Brunn. **(A)** *Caturus* sp., SNSB-BSPG 1993 XVIII P3. **(B)** *Amblysemius* sp., SNSB-BSPG 1993 XVIII P5. **(C)** *Ophiopsis muensteri*, SNSB-BSPG 1993 XVIII 12. *Ainia armata*, SNSB-BSPG 1993 XVIII P6 Scale bars are in 1 cm increments.

chycormiforms, and aspidorhynchiforms are here regarded as teleosts. In this context it is worth noticing that the name Teleosteomorpha proposed by Arratia (2001) to include her Teleostei and all its stem taxa is redundant because it is equivalent to Teleostei sensu Patterson (1977) or De Pinna (1996).

Aspidorhynchiforms and pycnodontiforms are poorly represented in the plattenkalks of Brunn, although these fishes are frequently found in other basins within the Solnhofen Archipelago (Lambers 1999, López-Arbarelo & Schröder 2014). The most complete and best preserved aspidorhynchid specimen from Brunn (SNSB-BSPG 1993 XVIII P7) most probably represents a new species of *Aspidorhynchus* (López-Arbarelo & Schröder pers. obs.), which shows some very interesting features, otherwise only known in *Aspidorhynchus arawaki* Brito, 1997, from the Upper Jurassic of Cuba. There is furthermore at least one specimen of *Belonostomus*, figured by Röper et al. (1996: Abb. 113).

Brunn pycnodontiforms (e.g., SNSB-BSPG 1993 XVIII P8; Textfig. 5A) are identified as *Gyrodus hexagonus* (Kriwet 2001). *Gyrodus* is probably the pycnodontiform genus with the broadest distribution, ranging from the Middle Jurassic to the Early Cretaceous, and from Europe to the Caribbean and the Pacific coast of South America. The species *G. hexagonus* is quite common in the Kimmeridgian and Tithonian localities of the Solnhofen Archipelago, but rare in the Kimmeridgian of Cerin (Lambers 1999, Kriwet 2001). Röper et al. (1996) also mention a specimen of *Procinetes*, which is a common genus found in Cerin (Lambers 1999), but this identification has yet to be confirmed.

Pachycormiforms are a still controversial and relatively poorly understood group of fishes that lived during the Jurassic and Cretaceous only. They are very abundant in the Early Jurassic and still diverse, though generally not as well represented in terms of number and state of preservation of the specimens in the Late Jurassic. An exceptionally well-preserved Late Jurassic pachycormiform is the Brunn specimen SNSB-BSPG 1993 XVIII-VFKO B16 (Textfig. 5B), which is the holotype of the species *Orthocormus roeperi* Arratia & Schultze, 2013. This complete and almost perfectly articulated specimen preserves a plethora of anatomical details, which are unknown in other pachycormiform taxa and are critical to solve the phylogenetic relationships of this very peculiar group of fishes. Although *O. roeperi* is so far only known in Brunn, Arratia & Schultze (2013) considered that it more closely resembles *O. taylori* Lambers, 1988, from the Late Kimmeridgian of Cerin, than *O. cornutus* Weitzel, 1930, from the Tithonian of Langenaltheim, which are the only two other species of this genus. Whether this close morphological similarity might reflect close phylogenetic relationships still needs to be tested in a cladistic analysis.

Siemensichthys, a rather common teleost in the Kimmeridgian and earliest Tithonian, is also relatively abundant in Brunn (Heyng et al. 2015). This genus, so far endemic to the Solnhofen Archipelago, includes two species, *S. macrocephalus* Agassiz, 1834, and *S. siemensis* Arratia, 2000. Although the specimens from Brunn have not yet been studied to the species level, the recent studies indicate closest phylogenetic relationships between *Siemensichthys* and two genera from the Kimmeridgian of Cerin, *Ankylopho-*

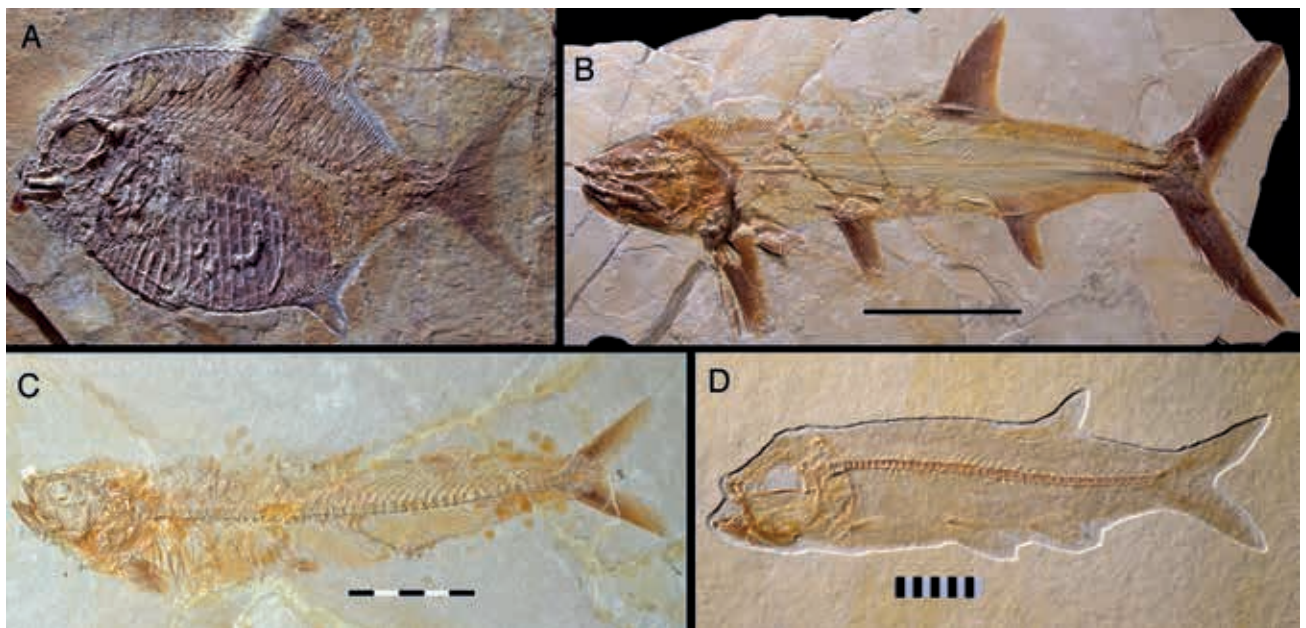


Figure 5: Teleosts from Brunn. **(A)** *Gyrodus hexagonus*, SNSB-BSPG 1993 XVIII P8. **(B)** *Orthocormus roeperi*, SNSB-BSPG 1993 XVIII VFKO B16. **(C)** *Allothrissops regleyi*, SNSB-BSPG 1993 XVIII 42 VFKO C129. **(D)** *Anaethalion cf. cirinensis*, SNSB-BSPG 1993 XVIII P9. Scale bars are 10cm (B), 5 cm (C) and 1 cm (D).

rus and *Lehmanophorus* (Arratia 2000, 2013). A rare taxon of basal teleosts is *Pleuropholis*, which is represented in Brunn by at least one specimen, figured by Röper et al. (1996: Abb. 111).

Ichthyodectiforms are particularly well represented in Brunn, including complete and almost fully articulated specimens of at least two species of *Allothrissops*. Based on the diagnosis and description of Nybelin (1964) and the illustration of the holotype in Thiollère (1854), two specimens (SNSB-BSPG 1993 XVIII VFKO C130 and SNSB-BSPG 1993 XVI-II 42 VFKO C129) represent the species *Allothrissops regleyi* (Textfig. 5C), which was previously only known from the Kimmeridgian of Cerin, France. The Brunn specimens, with approximately 230 mm and 260 mm of standard length are slightly larger than the specimens known from Cerin, which reach a standard length of 218 mm (Saint-Seine 1949: 304 specimens). Two other specimens (BSPG 1993 XVIII VFKO C132 and BSPG 1993 XVIII 42) probably represent *Allothrissops mesogaster*, which is a well-known species from several other Kimmeridgian and Tithonian localities of the Solnhofen Archipelago and from Nusplingen, but is so far unknown in Cerin.

Small teleosts are more abundant, although generally not so complete and well-preserved as the larger fishes listed in the previous paragraphs. Among them, at least four specimens resemble *Anaethalion cirinensis* Gaudant, 1968, very closely (Textfig. 5D). This species from Cerin is probably closely related to the recently described *Ebertichthys ettlingensis* Arratia, 2016, which, together with *Ascalabos voithii* Münster, 1839, form the family Ascalaboidae Arratia, 2016, thus representing an independent teleost clade restricted to the Late Jurassic European carbonate platform along the norther rim of the Tethys. *Anaethalion cirinensis* and the specimens cf. *A. cirinensis* from Brunn differ from *E. ettlingensis* mainly in the slightly higher number of vertebrae (40 and 43 vs. 38-39, respectively) and the proportionally slightly shorter caudal vertebral region (40-42% vs. 44%, respectively).

The most common fish in the Solnhofen Archipelago, *Tharsis dubius*, is also the most abundant actinopterygian in Brunn. However, although most of the specimens from Brunn are referable to *Tharsis dubius* (Blainville, 1918), many others certainly represent a different and new species of this genus.

More derived teleosts belonging to the crown-group Teleocephala are also abundant, including numerous specimens the salmoniforms *Leptolepides* and *Orthogonikleithrus*, at least one specimen representing a species of the elopomorph *Anaethalion*, and a single, but very nicely preserved specimen representing a new genus and species of still uncertain relationships.

3.4 Testudinata

Two partial turtle specimens from Brunn were stu-



Figure 6. Partial skeleton of a juvenile marine turtle, SNSB-BSPG 1993 XVIII VFKO-A1. Scale in mm.

died here. Röper et al. (1996) and Röper (1997) mentioned two further, extremely small and obviously largely disarticulated specimens from Plattenkalk layer 1, but these specimens have not been examined for this review; furthermore, a partial plastron of an indeterminate large turtle has been found recently. Both studied specimens are highly incomplete, making an identification difficult. A very small turtle specimen, SNSB-BSPG 1993 XVIII VFKO-A1 (Textfig. 6), preserves only the anterior half of the body, the left forelimb, the neck, and the lateral rim of the skull. The carapace of this specimen was only about 50 mm wide. The poor ossification of the carapace, as well as the unfinished appearance of the limb bones and the lack of any ossified carpals clearly indicate that this specimen represents an early ontogenetic stage. Small turtle specimens with separate ribs and a poorly ossified carapace from the Upper Jurassic laminated limestones of Germany have traditionally been assigned to *Aplax oberndorferi*, a species originally described on the basis of such an early juvenile turtle specimen by Meyer (1843). Although this species has often been considered to be a synonym of *Eurysternum wagleri* (Zittel 1877; Lapparent de Broin et al. 1996), Anquetin & Joyce (2014) recently did not find any evidence for such a referral and noted that such poorly ossified turtles should best be regarded as indeterminate (see also Joyce 2015). This view is followed here.

The second specimen, SNSB-BSPG 1993 XVIII P10 (Textfig. 7) probably represents a predation victim or the result of scavenging, as more than half of the carapace and plastron are missing, although there are no clear tooth marks. Most of the left costals and peripherals are preserved, but largely damaged, as is the left side of the plastron, which is largely hidden by the carapace elements, and the left scapula and humerus as well as the neck and skull are also present. As preserved, the carapace is c. 245 mm long, similar to the size of the type specimen of *Eurysternum wagleri* (Meyer 1839) and somewhat larger than the specimen of *Solnhofia* described by Joyce (2000) and the *Eurysternum* specimens described by



Figure 7: Partial skeleton of an indeterminate eurysternid turtle, SNSB-BSPG 1993 XVIII P10. Scale in cm.

Anquetin & Joyce (2014). In contrast to *Plesiochelys* (Anquetin et al. 2014) and *Palaeomedusa* (Joyce 2003), the carapace has well-developed peripheral fontanelles, and it lacks the strong ornamentation that is typical for *Platycheilus* (Cadena & Joyce 2015; Joyce 2015). The skull is short (about 20% of the length of the carapace), posteriorly broad and seems to have a short snout, similar to the situation in *Eurysternum* (Anquetin & Joyce 2014), but in contrast to *Solnhofia*, in which the skull is relatively larger and has a rather long snout (Joyce 2000). The carapace widens towards the posterior third, as it is also the case in *Solnhofia* (Joyce 2000) and *Eurysternum* (Anquetin & Joyce 2014), but the exact shape cannot be established, due to the incomplete preservation. However, the peripheral fontanelles seem to be relatively smaller than in *Eurysternum* and the carapace as a whole less broad than in *Solnhofia*. The latter is also a difference to *Tropidemys*, which has recently been identified in the Kimmeridgian of Wattendorf (Joyce 2015), but the presence or absence of the diagnostic dorsal midline keel of this taxon cannot be evaluated, as the neurals are not preserved. Due to the incomplete preservation, most of the diagnostic characters of *Eurysternum* (Anquetin & Joyce 2014) also cannot be evaluated. Although the posterior rim of the last preserved peripheral resembles the oblique margin of the 11th peripheral that forms the rim of the diagnostic pygal notch in this taxon (Anquetin & Joyce 2014), close examination of this margin reveals that it forms a sutural contact, and there is

a small fragment of a possible pygal plate preserved posteromedial to it. This indicates that no pygal notch might have been present in this specimen, but this interpretation should be seen with caution, as the incomplete preservation of the peripheral series and the poor preservation of the carapace in general leave some doubt whether the last visible lateral element really represent peripheral 11. Finally, the rather large size of the specimen argues against a referral to the rather small *Idiochelys*, but the possible lack of neural plates, which is typical for the latter genus (Joyce 2015), cannot be evaluated, due to the incomplete preservation.

In summary, SNSB-BSPG 1993 XVIII P10 seems to represent an eurysternid pancryptodire, but cannot be readily identified in any of the well-known taxa from the Upper Jurassic laminated limestones of southern Germany and might thus represent a new taxon. A more detailed analysis of this specimen and probably new finds are necessary to clarify the taxonomy of the eurysternid from Brunn.

3.5 Rhynchocephalia

Four specimens of rhynchocephalians have been recovered from the locality of Brunn so far, and, together with the type specimen of the pterosaur *Belubrunnus rothgaengeri*, represent the best-preserved reptile specimens found. All four specimens are complete and largely articulated, but compressed, as it is typical for fossils from the laminated limes-

Figure 8: Specimens of a new rhynchocephalian, similar to *Kallimodon*. (A, C) complete skeleton (A) and skull (C) of SNSB-BSPG 1993 XVIII 3. (B, D) complete skeleton (B) and skull (D) of SNSB-BSPG 1993 XVIII P11. Scale bars are in cm in A and B, 1 cm in C, and in mm in D.



tones. Based on a preliminary analysis, at least two and possibly three different taxa seem to be represented by these four specimens, indicating a considerable diversity of terrestrial rhynchocephalians in this locality. Two of these specimens were described briefly in a popular science article by Rauhut & Röper (2013).

Two specimens, SNSB-BSPG 1993 XVIII 3 and 1993 XVIII P11 (Textfig. 8), represent some of the largest rhynchocephalians known from the Late Jurassic of southern Germany (see Tischlinger & Rauhut 2015) and seem to belong to the same taxon. The former specimen (Textfig. 8A) has a total length of c. 380 mm, whereas the latter (Textfig. 8B) is even approximately 460 mm in total length. The limbs are notably short, with the forelimbs being 57% and 55% of the length of the presacral vertebral column, and the hindlimbs 92% and 82% of the same length, respectively. The body is elongate and slender. Both specimens are exposed in ventral view, so that only the ventral side of the skull and mainly the maxillary and premaxillary dentition are visible. However, SNSB-BSPG 1993 XVIII 3 has the lower jaw slightly displaced, so that the dentition of the right mandible is exposed in medial view (Textfig. 8C), and the left dentary dentition of SNSB-BSPG 1993 XVIII P11 is also visible in medial view (Textfig. 8D). The skull seems to have a rather long snout, as it is the case in *Kallimodon* (Cocude-Michel 1963). As in the Recent *Sphenodon* (Robinson 1976) there is only one, large premaxillary tooth. No successional teeth (Robinson 1976; Apesteguía et al. 2012) seem to be present in either maxillary or dentary. The lateral dentition of additional teeth is unusual in that it is strongly heterodont, with a gradual change from small, triangular teeth with well-developed posterior flanges anteriorly to increasingly transversely expanded, ridge-like teeth posteriorly, the posteriormost of which resemble the condition seen in opisthodontians in being wider transversely than long mesiodistally (see e.g. Throckmorton et al. 1981; Martínez et al. 2013; Apesteguía & Carballido 2014). However, also the most distal teeth retain a well-developed posterior flange

lingually. In contrast to most rhynchocephalians, the tooth row on the palatine seems to be poorly developed or even absent. The mesial dentary teeth are low, with well-developed anterior flanges, but distal teeth become higher, triangular in outline and with relatively shorter anterior flanges. The mandibular articulation of the mandible shows a small concavity, in contrast to the situation in derived sphenodontids, which show a longitudinal ridge in this region (e.g. Rauhut et al. 2012a).

The only other rhynchocephalians from the Upper Jurassic laminated limestones of southern Germany that reach a similar length as these two specimens are the type specimen of *Piocormus laticeps* (Wagner 1852; Cocude-Michel 1967), a specimen referred to *Sapheosaurus* from the collection of Helmut Tischlinger (Tischlinger & Rauhut 2015: fig. 840) and two undescribed specimens from the Kimmeridgian of Wattendorf (Mäuser 2015: fig. 1027; Tischlinger & Rauhut 2015: fig. 838) and Painten (Tischlinger & Rauhut 2015: fig. 839). However, the former three of these specimens differ from SNSB-BSPG 1993 XVIII 3 and 1993 XVIII P11 in the broader, more robust body, whereas the specimen from Painten shows a very different dentition. In general proportions, the specimens from Brunn are similar to the holotype and a referred specimen of *Kallimodon* (Table 1; Cocude-Michel 1963), but differ from these in the considerably larger body size (the type of *Kallimodon*, one of the largest specimens referred to this genus known, is c. 180 mm long as preserved, and was certainly no more than 250 mm long when considering the missing tip of the tail) and the dentition. Thus, these specimens cannot be referred to any of the known species of rhynchocephalians from the laminated limestones of southern Germany and thus most probably represent a new taxon, possibly related to *Kallimodon*. However, as the latter genus is also in need of revision (Rauhut & López-Arbarello 2016), no new name is proposed here, pending such a revision.

The specimen SNSB-BSPG 1993 XVIII 4 also represents a rather large animal, with a total length of 345 mm (Textfig. 9). The body is more robust than in



Figure 9: Skeleton of a new sphenodontine rhynchocephalian, SNSB-BSPG 1993 XVIII 4. Scale in cm.

the specimens described above, and the limbs relatively longer, with the hindlimbs slightly exceeding the presacral vertebral column in length; the ratios of limb lengths to presacral vertebral column length are intermediate between that seen in *Kallimodon* and that of *Homoeosaurus* (Table 1). As in the specimens described above, the tail is very long, accounting for c. 220 mm of the length of the animal, with the final c. 50 mm being regenerated (see Rauhut & Röper 2013: abb. 9), indicating the capability of tail autotomy, as it has been described for other Jurassic rhynchocephalians (Tischlinger & Wild 2009).

As in the specimens described above, the skull is visible in ventral view, with the tooth-bearing elements being slightly disarticulated and the mandibles displaced (Textfig. 10). The skull seems to have been relatively shorter and broader than in *Kallimodon* and the specimens described above. The dentition differs markedly from that of other rhynchocephalians known from the Late Jurassic limestones of southern Germany (see Cocude-Michel 1963; Carroll & Wild 1994; Rauhut et al. 2012; Rauhut & López-Arbarello 2016). The premaxilla bears three teeth, with the mesial two being smaller, incisor-like and closely appressed, whereas the third is larger, canine-like and separated from the more mesial teeth by a deep cleft. The lateral maxillary and dentary dentitions show some remarkable similarities to that of the recent *Sphenodon* (Robinson 1976). The anterior part of the maxilla bears three to four successional teeth, with the last of these being enlarged and fang-like, followed by a small row of very small and largely worn hatchling teeth. Posterior to this row, several large, conical additional teeth are present. The palate also shows a row of robust, but slightly smaller teeth that was apparently parallel to the maxillary tooth row, as in most derived rhyn-



Figure 10: Skull of a new sphenodontine rhynchocephalian, SNSB-BSPG 1993 XVIII 4. Abbreviations: ld, left dentary; lm, left maxilla; lpal, left palatine; lpm, left premaxilla; rd, right dentary; rm, right maxilla; rpal, right palatine; rpm, right premaxilla. Scale in cm.

chocephalians. The anterior end of the dentary also shows some successional teeth, including two smaller mesial teeth and an enlarged, canine-like tooth. Posteriorly follows a row of conical additional teeth, which gradually increase in size posteriorly, as in the modern *Sphenodon*. The jaw articulation in this specimen is formed by a longitudinal ridge on the articular, as in derived sphenodontians.

This specimen clearly differs from all other rhynchocephalians described from the Late Jurassic limestones of southern Germany and thus certainly represents a new taxon. Its general characteristics,

Table 1: Selected measurements of the rhynchocephalian specimens from Brunn in comparison to other rhynchocephalian specimens from the Late Jurassic of the Solnhofen Archipelago: SNSB-BSPG 1887 VI 502: neotype of *Homoeosaurus maximiliani*; SNSB-BSPG 1887 VI 1: holotype of *Kallimodon pulchellus*.

	1993 XVIII 3	1993 XVIII P11	1993 XVIII 4	1993 XVIII P12	1887 VI 502	1887 VI 1
Humerus	21,4	22,7	17,4	7,4	18	16
lower arm	14,8	15,9	15,7	5,7	15,5	11
Manus	17,9	21,8	16,1	7,4	16	16
forelimb	57,1	68,6	55,7	23,8	55	46
Femur	29,3	33,2	26,8	9,5	23,5	20,5
lower leg	22,1	22,5	19,6	9,5	22	16,5
pes	32,1	34	27	13,1	27	29
hindlimb	92,9	102,3	81,7	34	78	74
presacral vertebrae	100,7	125,5	73,3	25,5	66	87
Forelimb/hindlimb	0,61	0,67	0,68	0,70	0,71	0,62
forelimb/presacral	0,57	0,55	0,76	0,93	0,83	0,53
hindlimb/presacral	0,92	0,82	1,11	1,33	1,18	0,85



Figure 11: Skull (inset) and skeleton of a juvenile rhynchocephalian, SNSB- BSPG 1993 XVIII P12. Scales in mm.

especially of its dentition, resemble the condition in *Sphenodon* and other sphenodontines (e.g. Reynolds 1996, 2003), indicating that this specimen might represent a sphenodontine sphenodontid. However, as Apesteguía et al. (2012) pointed out, the dentition of rhynchocephalians and especially the possible homologies of caniniform successional teeth need further study. Pending a more detailed analysis of this specimen, we therefore only refer it to Sphenodontidae incertae sedis here.

The smallest specimen, SNSB-BSPG 1993 XVIII P12, is only c. 80 mm long and represents a juvenile individual, as demonstrated by the generally poor state of ossification of the limbs, especially the wrist (Textfig. 11). The limbs are remarkable long in comparison to the vertebral column, even more so than in *Homoeosaurus*, which this specimen most closely resembles in respect to its proportions (Table 1). The dentition is highly unusual. The premaxilla bears three to four well separated teeth, and the maxilla shows a row of conical teeth. Interestingly, for most of the length of the maxillary tooth row, the dentition shows alternating large and small teeth, as it is typical for reptiles with active tooth replacement, which

only occurs in the hatchling dentition in *Sphenodon* (Robinson 1976). Thus, only the last two to three maxillary teeth of this specimen might be true additional teeth, also testifying to its early ontogenetic stage. The dentary teeth are more uniform, being low and pentagonal in outline mesially and becoming higher, more pointed, and triangular towards the back of the tooth row.

As with the other specimens from Brunn, this specimen cannot readily be referred to any of the known rhynchocephalians known from the Upper Jurassic laminated limestones of southern Germany. The dentition is clearly juvenile and therefore cannot be readily compared to any of the taxa known from adult specimens. The general proportions, especially the remarkable long limbs, resemble the condition in *Homoeosaurus*. However, as basically nothing is known about allometric changes during the ontogeny of Mesozoic rhynchocephalians, a referral to this taxon should be seen as tentative. Given the very young ontogenetic stage of the specimen, it also cannot be excluded that it might simply represent a juvenile of one of the other taxa present in Brunn, especially that represented by SNSB-BSPG 1993 XVIII 4.

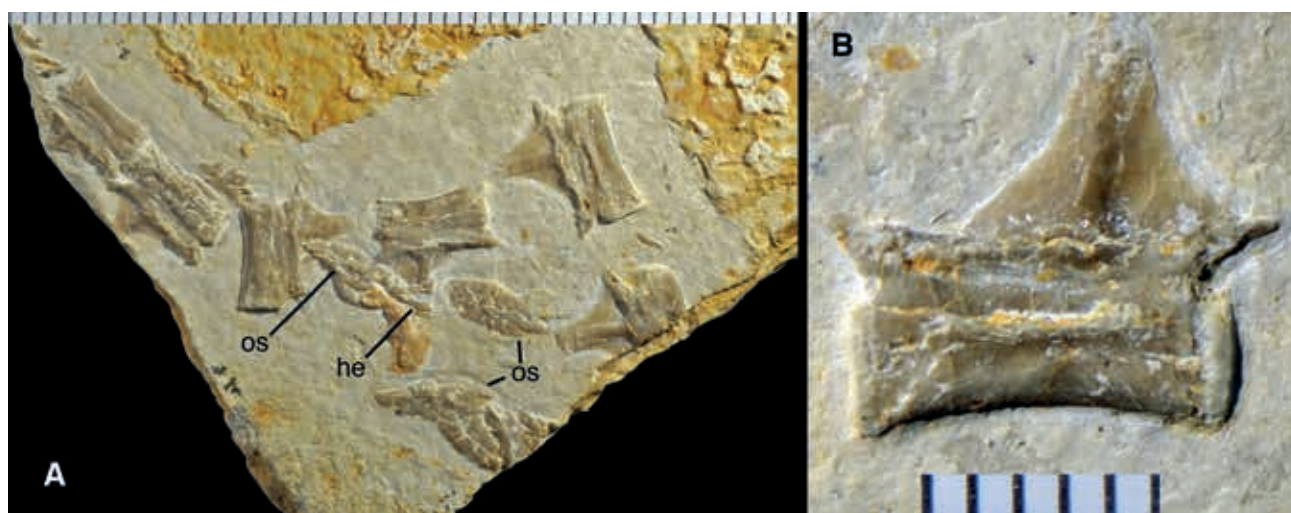


Figure 12: Remains of an atoposaurid crocodyliform, SNSB-BSPG 1993 XVIII VFKO-A5. **(A)** slab with several caudal vertebrae, hemapophyses and osteoderms. **(B)** detail of a caudal vertebra in lateral view. Abbreviations: he, hemapophysis; os, osteoderm. Scales in mm.

3.6 Crocodylomorpha

One specimen, SNSB-BSPG 1993 XVIII VFKO-A5 represents a crocodyliform (Textfig. 12). The specimen consists of a small limestone slab containing six mid-caudal vertebrae, some chevrons, and several osteoderms (Textfig. 12A), which are clearly crocodylomorph. The caudal vertebrae (Textfig. 12B) are very small, with the centrum of the well-preserved anteriormost complete caudal being 8 mm long and 3 mm high. They have low, strongly elongate, amphicoelous centra that are only slightly constricted in lateral view. The neural arch is low and extends over almost the entire length of the centrum, and the pre- and postzygapophyses overhang the centrum as small, triangular processes anteriorly and posteriorly. The neural spine is an erect, moderately high, triangular process, in which a slightly thickened central part is connected to the bases of the zygapophyses by well-developed pre- and postspinal laminae. Transverse processes are not present, there is only a small lateral ridge at the basis of the thickened central portion of the neural spine. The preserved chevrons are short, V-shaped elements in which the hemal canal is not bridged proximally, but the left and right rami remain separated up to their connection with the vertebrae. The osteoderms are elongate, with notably convex lateral(?) and straight medial(?) margins. There is a wide, anteriorly rounded anterior(?) and a smaller, more pointed posterior(?) process, which are connected by a low, longitudinal ridge across the external surface of the osteoderm. The external surface shows the typical groove pattern of crocodyliform osteoderms.

The low and elongate shape of the caudal vertebral centra is typical for neosuchian crocodyliform mid-caudal vertebrae, as are the relatively short, slightly overhanging zygapophyses and the moderately high, erect neural spine with well-developed an-



Figure 13: Tooth of the teleosauroid crocodyliform cf. *Machimosaurus* sp. Scale bar is 5 mm.

terior and posterior laminae (e.g. O'Neill et al. 1981; Lio et al. 2012; OR, pers. obs.). The general shape of these vertebrae closely corresponds to a caudal vertebra of *Alligatorellus* described by Schwarz-Wings et al. (2011), and the shape of the hemapophyses and the osteoderms, and the size are also consistent with an atoposaurid identification (Wellnhofer 1971; Schwarz-Wings et al. 2011: 199, 201). Thus, this specimen is referred to an indeterminate atoposaurid.

A second, probable crocodyliform specimen, SNSB-BSPG 1993 XVIII P14, consists of a single, strongly worn tooth (Textfig. 13). The crown has a round cross-section and is considerably recurved, but the tip is worn down to a flat stump, testifying

of a durophagous diet. Mesial and distal carinae are absent, but the tooth shows rather well-developed longitudinal striations that are mainly parallel, although some converge towards the apex. As the apex is worn away, it cannot be said whether the striations anastomose apically, as it is the case in *Machimosaurus* and “*Steneosaurus*” *obtusidens* (Young et al. 2014; Foffa et al. 2015).

Teeth with a rounded cross-section and well-developed striations are usually found in plesiosaurs (e.g. Massare 1987) and several groups of crocodyliforms, including teleosaurid thalattosuchians (Vignaud 1997; Mueller-Töwe 2006; Foffa et al. 2015). However, sauropterygian teeth are usually more slender and lack the extensive wear seen in this specimen (Massare 1987). Furthermore, this clade is exceedingly rare in the lithographic limestones of southern Germany, with only a single tooth having been reported from the Solnhofen Archipelago (Wagner 1852). Within crocodyliforms, the marine thalattosuchians are the best represented group within the Solnhofen Archipelago (Frey & Tischlinger 2015). Whereas the metriorhynchid genera *Cricosaurus*, *Geosaurus* and *Dakosaurus* usually have more flattened teeth with well-developed, often serrated carinae and no or only weakly developed striations (Young & Andrade 2009; Andrade et al. 2010; Young et al. 2010, 2012), many teleosaurids have well-developed longitudinal striations on the tooth crowns (Vignaud 1997). The teeth in most teleosaurids are more slender and usually do not show a large amount of wear, but the durophagous “*Steneosaurus*” *obtusidens* and *Machimosaurus* have stout teeth with rounded cross sections and well-developed striations (Young et al. 2014; Foffa et al. 2015). “*Steneosaurus*” *obtusidens* has weakly developed carinae in the teeth, while these are missing in at least some teeth of *Machimosaurus*, so we tentatively refer this tooth to the latter genus. Although *Machimosaurus* is a common taxon in the Late Jurassic of Europe (Young et al. 2014), this is only the second record of this genus in the Solnhofen Archipelago, the first being a single tooth from the Tithonian Mörsheim Formation of Mühldorf (Heyng et al. 2011).

3.7 Pterosauria

Given that pterosaurs represent the most common group of terrestrial tetrapods in many of the Bavarian Plattenkalk localities, surprisingly few specimens have so far been recovered from Brunn. The most remarkably specimen is certainly the complete, articulated skeleton of a juvenile rhamphorhynchid, SNSB-BSPG 1993 XVIII 2 (Textfig. 14), which was described as a new genus and species, *Bellubrunnus rothgaengeri*, by Hone et al. (2012). Due to the early ontogenetic stage of the specimen, its validity as a distinct taxon has repeatedly been questioned. Thus, Tischlinger & Frey (2015) recently noted that the specimen is remarkably similar to *Scaphognathus*



Figure 14: Holotype specimen of *Bellubrunnus rothgaengeri*, SNSB-BSPG 1993 XVIII 2. Scale bar is 1 cm.

thus, for which little ontogenetic data exists, whereas O’Sullivan & Martill (2015) discuss that several of the supposedly diagnostic characters of *Bellubrunnus rothgaengeri* are also found in juvenile specimens of *Rhamphorhynchus*, while others are difficult to verify and might reflect preservation. The latter authors conclude that „For now, we consider *Bellebrunnus* [sic.] to be sufficiently similar to *Rhamphorhynchus* to be considered congeneric based on the current diagnosis for the genus“ (O’Sullivan & Martill 2015: 399), but note that two other characters, the lack of stiffening rods formed by the zygapophyses and the chevrons in the tail and the anteriorly curved last wing phalanx, indicate that it might represent a species distinct from *Rhamphorhynchus muensteri*. The former character, the lack of stiffening rods in the tail, might also be an ontogenetic character, as these rods seem to be mainly formed by ossified tendons in animals in which such a stiffening of the tail is present (e.g. Ostrom 1969). However, the ultimate wing phalanx of *Bellubrunnus rothgaengeri* is indeed unique in that it is notably curved anteriorly, instead of slightly posteriorly, as it is the case in most pterosaurs. As these phalanges are preserved in both sides of the wing and show identical morphology, this difference can furthermore also not be accounted for by preservation, and there is currently no evidence for ontogenetic changes in the curvature of the wing phalanx in pterosaurs. Thus, we regard the species *B. rothgaengeri* as valid, and, given the uncertainty of ontogenetic changes in other rhamphorhynchids, also provisionally retain the genus *Bellubrunnus*, until ontogenetic studies and/or unambiguously shared derived characters conclusively show that the species can be referred to either *Rhamphorhynchus* or *Scaphognathus*. It should be noted, though, that the genus *Rhamphorhynchus* is in need of revision, as numerous new finds and recent developments in our



Figure 15: (A) Anterior end of the snout of a new gnathosaurine ctenochasmatid pterosaur in ventral view. (B) Detail of the dentition, showing marked carina in mesial teeth and enamel ornamentation in more distal teeth. Scale bars are in mm.

understanding of pterosaur anatomy, diversity, taxonomy and phylogeny make a re-assessment of the taxonomic conclusions of the last major revision of this taxon (Wellnhofer 1975a) necessary.

Apart from *Bellubrunnus*, only a few additional pterosaur specimens have been found, a section of conjoined jaws, two isolated appendicular elements and a small assemblage of broken wing phalanges. Unfortunately, however, the latter assemblage is poorly preserved, so these bones cannot currently be identified beyond the level of Pterosauria indet.

The jaw represents the anterior end of the snout, including the anterior ends of the maxillae, the palatines, and the premaxillae (Textfig. 15). The snout is very slender, with almost parallel margins in the region of the anterior maxillae. The tip of the snout expands slightly to form a small terminal rosette (Textfig. 15A), similar to the situation in *Gnathosaurus* (Wellnhofer 1970) and *Plataleorhynchus* (Howse & Milner 1995), though less conspicuous. Sutures between the different elements are difficult to establish and they might be partially fused, as in other pterosaurs (e.g. Howse & Milner 1995). Whereas the palatines are separate posteriorly, their anterior parts seem to be fused and form an anteriorly tapering plate of bone between the maxillae, as in *Plataleorhynchus* (Howse & Milner 1995). Although no clear suture between the premaxillae and maxillae is visible, the anterior extend of the palatines indicates that the premaxillae are relatively shorter than in other ctenochasmatids (Wellnhofer 1970; Dong 1983; Howse & Milner 1995; Unwin 2002; Bennett 2007a) and probably bore only four to five tooth positions, with the anteriormost teeth pointing anteriorly.

The right maxilla preserves six to seven tooth positions. The rims of the alveoli are somewhat expanded, forming a “collar” for the tooth, as in *Plataleorhynchus* (Howse & Milner 1995) and, to a lesser degree, in *Gnathosaurus* (Wellnhofer 1970), giving the rostrum a slightly festooned appearance. The teeth are relatively widely spaced, with the distance between alveoli being more than the width of the

tooth bases. The alveoli face laterally and anteriorly, as in *Gnathosaurus* (Wellnhofer 1970). The preserved teeth represent mainly or even exclusively maxillary teeth, depending on the position of the premaxillary-maxillary suture. The anterior maxillary dentition is notable for a marked change in tooth morphology from the posteriormost preserved to the first maxillary tooth. Although the teeth are generally incomplete, and most lack the tip, the posterior teeth seem to be lower and are considerably more robust than the anterior teeth. All teeth are pointed and strongly recurved, the anterior teeth with a notable kink at about half-height, basal to which the tooth seems to be slightly bulbous, whereas the apical part is slender and pointed. The more distal teeth show a well-developed, granulate ornamentation on the enamel (Textfig. 15B), similar to the condition found in many sauropods (e.g. Holwerda et al. 2015); this ornamentation is more weakly developed in the more mesial teeth. The slender mesial teeth have a marked mesial carina that is slightly inclined lingually, resulting in a longitudinal groove on the lingual side adjacent to the carina (Textfig. 15B). Judged by the size of the alveoli, the premaxillary teeth seem to have been somewhat larger than the anterior maxillary teeth, though not to the degree seen in *Cearadactylus* (Unwin 2002).

Based on the narrow, parallel-sided rostrum, the more laterally than ventrally pointing teeth and the shape of the anterior maxillary teeth, this specimen can be referred to the Ctenochasmatidae (see Wellnhofer 1978; Unwin 2002). Within ctenochasmatids, Unwin (2002) distinguished the Ctenochasmatinae from the Gnathosaurinae (see also Andres & Ji 2008; Andres et al. 2014), with the latter being characterized by a rounded expansion of the anterior end of the rostrum. The fact that the specimen from Brunn shows such an expansion, though less well developed than in *Gnathosaurus* and *Plataleorhynchus*, indicates that it might be referable to that subfamily. However, it differs considerably from all other gnathosaurines in the short premaxilla with few teeth,



Figure 16: Isolated limb bones of pterodactyloid pterosaurs from Brunn. **(A)** Right humerus of an unidentified pterodactyloid, SNSB-BSPG 1993 XVIII VFKO-A3 in posterior view. **(B)** Right femur of *Ardeadactylus* cf. *longicollum*, SNSB-BSPG 1993 XVIII P13, in posterior view. Scale in mm.

the rapid change in tooth morphology in the anterior maxilla, and the ornamented enamel in more distal teeth and marked mesial carina in mesial teeth and thus certainly represents a new taxon. A formal description of the new taxon will be presented elsewhere.

The two appendicular specimens, an isolated right humerus and an isolated right femur, are remarkable for their large size (Textfig. 16). The right humerus SNSB-BSPG 1993 XVIII VFKO-A3 is 100.2 mm long and robust (Textfig. 16A). The proximal end has a saddle-shaped articular surface, as it is typical for pterosaur humeri. Thus, the articular end is concave transversely, but convex anteroposteriorly. A well-developed, elongate, subrectangular internal tuberosity is present, but the deltopectoral crest, which was found to be of systematic value in pterosaur phylogenies (e.g. Unwin 2003; Andres et al. 2014), is, unfortunately, largely hidden in the matrix. However, judged by the visible parts, it was most probably rather moderately developed, and not strongly expanded anteriorly, as it is the case in *Rhamphorhynchus* and other rhamphorhynchids (Wellnhofer 1975a, b, 1978; Padian 2008; Andres et al. 2010). No pneumatic foramen is visible on the posterior side of the proximal humerus. The shaft is stout and straight, and expands distally towards the strongly laterally

expanded distal articular end. The latter seems to be twisted in respect to the proximal end, so that it faces slightly anterolaterally.

In comparison with the humeri of other pterosaurs known from the Upper Jurassic laminated limestones of southern Germany, this element is notably large and robust. Indeed, this element is considerably longer than any humerus of non-pterodactyloid pterosaurs from the Upper Jurassic laminated limestones of southern Germany measured by Wellnhofer (1975a). The specimen furthermore differs from the common rhamphorhynchids of the laminated limestones of southern Germany in the less expanded deltopectoral crest of the humerus and the also less expanded internal tuberosity at the proximal end (Wellnhofer 1975b). The only non-rhamphorhynchid “rhamphorhynchoid” from the Upper Jurassic of southern Germany, *Anurognathus*, has a less strongly expanded deltopectoral crest, but differs from SNSB-BSPG 1993 XVIII VFKO-A3a in the also considerably expanded internal tuberosity (Wellnhofer 1975a; Bennett 2007b). In *Bellubrunnus*, both the deltopectoral crest and the internal tuberosity are less expanded than in other rhamphorhynchids (Hone et al. 2012), but still more so than in the current specimen. Furthermore, the condition in *Bellubrunnus* most probably reflects the early ontogenetic stage of the specimen, and adults of this taxon might have been more similar to *Rhamphorhynchus* in humeral morphology.

In terms of size, the specimen from Brunn falls within the range of the largest specimens of pterodactyloids listed in Wellnhofer (1970). Apart from a now lost specimen referred to “*Pterodactylus*” *grandis* from the Mörsheim Formation (Wellnhofer 1970), only one described specimen from the Late Juras-

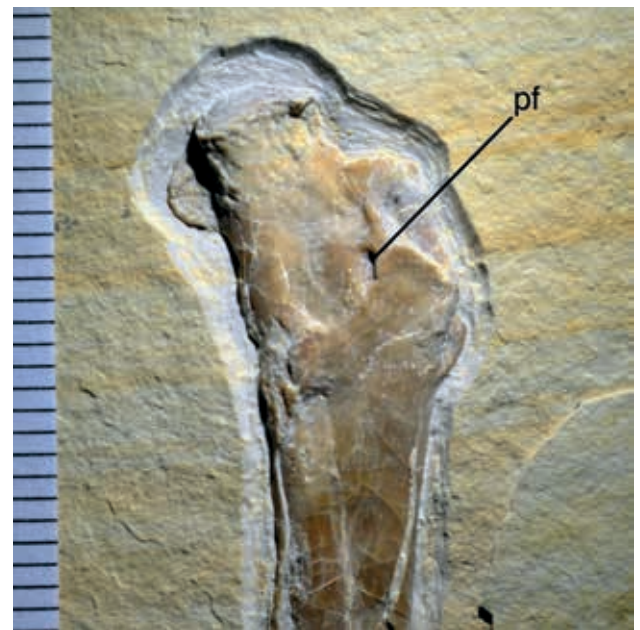


Figure 17: Proximal end of right femur of *Ardeadactylus* cf. *longicollum*, SNSB-BSPG 1993 XVIII P13. Abbreviation: pf, pneumatic foramen. Scale in mm.

sic laminated limestones of southern Germany has a longer humerus, an isolated wing from the Solnhofen Formation at Schernfeld (JME 1963 1a) that was referred to as "*Pterodactylus*" sp. by Wellnhofer (1970), which exceeds the specimen from Brunn by 16 mm. The humerus of this specimen is furthermore similar to SNSB-BSPG 1993 XVIII VFKO-A3a in being stout, having a moderately developed internal tuberosity and deltopectoral crest and gradually expanding distally. Thus, we refer this specimen to an indeterminate pterydactyloid. Based on the unusually large size, it might represent the same taxon as the femur described below.

The right femur SNSB-BSPG 1993 XVIII P13 is 87.6 mm long and more slender than the humerus described above (Textfig. 16B). It has a well set-off femoral head that is more proximally than medially directed, as it is typical for pterosaurs (Wellnhofer 1978). The shaft is straight and of subequal width throughout its length in anterior view. The external trochanter (Wellnhofer 1975b; greater trochanter or trochanter major of other authors, e.g. Bennett 2001; Cordoníu et al. 2006) is well developed and subrectangular in shape, starting at the lateral side of the base of the femoral head and extending for some 9 mm distally. In contrast to many pterosaurs, it does not fade gradually into the femoral shaft distally, but is clearly offset by an oblique step (Textfig. 17). At about half-height of the external trochanter, a large pneumatic foramen pierces the base of the trochanter (Textfig. 17), in a very similar position as a large foramen in *Pteranodon*, which Bennett (2001) identified as a nutrient foramen. However, nutrient foramina in archosaur femora are usually placed more distally and relatively smaller, so that we consider an interpretation of this opening as a pneumatic foramen more likely. The distal end of the femur is expanded, more so medially than laterally. Unfortunately, the articular end is eroded, so nothing can be said about the morphology of the distal condyles.

Whereas the strongly offset, proximally directed femoral head characterizes this specimen as a pterosaur element, the rectangular external trochanter is unusual, especially in respect to the angular appearance of the distal end of the trochanter. In the vast majority of pterosaurs, including *Rhamphorhynchus* (Wellnhofer 1975b), *Bellubrunnus* (Hone et al. 2012), *Anurognathus* (Bennett 2007b; Tischlinger & Frey 2015), *Pterodactylus* (e.g. SNSB-BSPG 1937 I 18), *Germanodactylus* (SNSB-BSPG AS I 745, SNSB-BSPG 1892 IV 1), *Aurorazhdarcho* (Frey et al. 2011), and *Cycnorhamphus* (Bennett 2013a), the external trochanter fades gradually into the femoral shaft distally. A morphology similar to that seen in the specimen from Brunn has so far only been illustrated for a specimen of *Ardeadactylus longicollum* (Wellnhofer 1970: Abb. 11b; see also Bennett 2013b). Although the femur of the latter taxon seems to differ in the slightly more elongate and less strongly proximally directed femoral head, we therefore refer this speci-



Figure 18: Reptilia indet., SNSB-BSPG 1993 XVIII 2/2009, two dorsal vertebrae in posterior view. Scale in mm.

men to *Ardeadactylus* cf. *longicollum*. Unfortunately, in the neotype of *Ardeadactylus longicollum*, a specimen from the Kimmeridgian of Nusplingen (Wellnhofer 1970), the proximal ends of both femora are covered by pelvic elements (Plieninger 1907).

3.8 Reptilia indet.

One specimen, SNSB-BSPG 1993 XVIII 2/2009 (Textfig. 18), cannot currently be confidently identified in any clade. It consists of two small dorsal vertebrae that are poorly preserved and exposed in posterior view. Interestingly, the vertebral centra are slightly procoelous, as it is found in eusuchian crocodyliforms and squamates. The neural arch is rather high, with the distance between the dorsal rim of the centrum and the transverse processes being similar to centrum height. Transverse processes are strongly developed and laterally and slightly dorsally directed. No details of the zygapophyseal articulations are preserved. The neural spine is rather low (lower than the neural arch) and posterodorsally directed, being hook-shaped, pointed dorsally. Although the shape of the vertebral centrum, the stout transverse processes and the relatively low, posteriorly inclined neural spine indicate a terrestrial reptile, little can be said about the affinities of these elements. In respect to size, these vertebrae, which are approximately 11-12 mm high, would fit an atoposaurid crocodylomorph (Wellnhofer 1971; Frey & Tischlinger 2015), but would be rather large for any squamate known from the laminated limestones of southern Germany so far (see Tischlinger & Rauhut 2015).

4. Discussion

Despite the rather short time since the discovery and excavations of the locality Brunn, this site has yielded a remarkably diverse vertebrate fauna, reflecting the much higher density of fossils in the

Plattenkalk intercalations at this locality than in the Altmühltal Formation, as pointed out by Röper et al. (1996) and Röper (1997). The vast majority of specimens recovered yet need detailed study and analysis, but we may offer some preliminary thoughts on the significance of the fauna here.

The general composition of the fish fauna of Brunn, with a great majority of small teleosts and less represented aspidorhynchiforms, pachycormiforms, pycnodontiforms, ginglymodians, and halecomorphs does not seem to differ significantly from other localities within the Solnhofen Archipelago (see e.g. Ebert et al. 2015), except for the scarcity of chondrichthyans, which are relatively abundant in other sub-basins. A closer look at the taxonomic composition reveals, however, significant differences with the Tithonian localities, and close resemblance with other Kimmeridgian localities.

The only identified shark, *Palaeoscyllium*, represents a taxon that was originally described from the Solnhofen Member of the Altmühltal Formation (Wagner 1857), but even the type species, *P. formosum*, also has a wide distribution in the Kimmeridgian of Europe (Kriwet & Klug 2004). Furthermore, other species of this genus range from the Bathonian to the Aptian (Kriwet & Klug 2004), so, pending a detailed study and identification of the specimen from Brunn on the species level, nothing can be said about its evolutionary significance. However, the rarity of the fully marine chondrichthyans supports the interpretation of Brunn as a rather isolated, marginal marine, probably lagoonal environment (Röper & Rothgaenger 1997; Heyng et al. 2015).

The association of actinopterygian fishes from Brunn seems to be more similar to that of the Kimmeridgian limestones of Cerin (Wenz et al. 1994) and other Kimmeridgian faunas of the Solnhofen Archipelago (e.g. Painten, Kelheim, Ettling) than to the „typical“ Solnhofen fauna in the vicinities of Eichstätt and Solnhofen, as already suggested by Röper (1997). Many of the taxa that could be identified on species level are otherwise mainly or exclusively found in Kimmeridgian localities. This is the case with the halecomorph *Ophiopsis muensteri*, which is also present in Kelheim, Ettling and Cerin (Lane & Ebert 2012). Likewise, the halecomorph *Ainia armata* is also present in Kelheim and Cerin. *Macrosemius fourneti* is found in Cerin and the lower, Kimmeridgian section of the locality of Painten, and differs from *Macrosemius rostratus* from the Tithonian localities. In respect to the teleosts, *Allothrissops regleyi* is also present in Cerin, whereas *Allothrissops mesogaster* (Agassiz, 1834) is the species represented in the Tithonian localities. Likewise *Anaethalion cirinensis* is a species that is also known from Cerin and Ettling. A similar actinopterygian fauna also seems to be present in the Kimmeridgian of Nusplingen (ALA, pers. obs.), further indicating that there was some faunal change in actinopterygian faunas from the Kimmeridgian to the Tithonian, as argued by López-Arbarello



Figure 19: Proximal end of the femur of cf. *Ardeadactylus* sp. from the Mörsheim Formation of Daiting, SNSB-BSPG 1977 XIX 39. Abbreviation: pf, pneumatic foramen. Scale bar is 1 cm.

& Schröder (2014) for the genus *Aspidorhynchus*.

Concerning the reptile fauna, a rather high level of endemism of the Brunn fauna is striking. None of the more complete, articulated reptile specimens can be referred to any species known from other localities within the Solnhofen Archipelago. This is the case of the eurysternid turtle, which probably represents a new taxon, although further study of this material is necessary to confirm this. In the rhynchocephalians, at least two new taxa are clearly present, one represented by the specimens SNSB-BSPG 1993 XVIII 3 and SNSB-BSPG 1993 XVIII P11, and the other by SNSB-BSPG 1993 XVIII 4. Whereas the former taxon seems to be similar and probably related to *Kallimodon* (see Cocude-Michel 1963; Rauhut & Röper 2013), the second specimen does not show close resemblance to any other rhynchocephalians known from the Late Jurassic of Europe, and seems to rather resemble sphenodontines on the lineage towards the recent *Sphenodon*, such as *Cynosphenodon* (Reynoso 1996; see also Cau et al. 2014). The juvenile specimen can also not be referred to any known taxon, although it cannot be ruled out that this is due to its early ontogenetic stage. As noted above, it may also be possible that it represents a juvenile of one of the other two taxa from Brunn, especially SNSB-BSPG 1993 XVIII 4, to which it is more similar in respect to its general proportions and the number of premaxillary teeth. However, both of these characters might be subject to ontogenetic variation (see Robinson 1976).

In the pterosaurs, *Bellubrunnus rothgaengeri* seems to represent an endemic taxon that has so far only been identified in Brunn, and the isolated gnathosaurine rostrum also represents a new taxon

that has otherwise not been reported from the Solnhofen Archipelago. The second identified taxon, *Ardeadactylus*, is, however, present in other localities. Wellnhofer (1970) referred a total of six specimens to *Ardeadactylus longicollum* (*Pterodactylus longicollum* in Wellnhofer 1970), ranging from the Kimmeridgian of Nusplingen to the Tithonian Mörsheim Formation of Daiting. However, three of these specimens were lost during WW II, and the referral of one other specimen, consisting only of a femur and incomplete tibia, is doubtful (Bennett 2013b). As only the original illustrations of the lost specimens exist, only two specimens can thus currently be regarded as being securely referable to this species (Bennett 2013b). Interestingly, both of these specimens come from Kimmeridgian localities, the neotype from the *hoelderi* horizon of the Ulmense Ammonite Sub-zone of Nusplingen and the referred specimen from the *rebouletianum* horizon of the Ulmense Sub-zone of Schamhaupten (Wellnhofer 1970; Schweigert 2015). Being derived from the Subeumela Sub-zone of the Late Kimmeridgian, the record from the locality Brunn is thus the currently oldest record of the genus *Ardeadactylus* (Schweigert 2015). Given that all specimens referred to this genus so far come from the Kimmeridgian begs the question whether this might also indicate some temporal stratigraphic segregation of the pterosaur faunas in the Solnhofen Archipelago. This might be contradicted by the now lost original specimens of *Ardeadactylus longicollum* (Wellnhofer 1970). Furthermore, there is an undescribed specimen from the locality of Daiting in the Mörsheim Formation (Mörsheimensis Subzone of the Lower Tithonian; Schweigert 2015) in the collections of the BSPG (SNSB-BSPG 1977 XIX 39) that consists only of the sacrum, pelvis and left hindlimb of a very large pterosaur. This specimen, which is currently identified as “*Pterodactylus grandipelvis*”, shows the same, angular external trochanter in the femur (Textfig. 19) that is also seen in the specimen from Schamhaupten (Wellnhofer 1970) and the specimen from Brunn. As the specimen with a femoral length of c. 100 mm also falls within the size range reported for *Ardeadactylus longicollum* (Wellnhofer 1970), it is probably also referable to this genus. However, as with the femur of the Schamhaupten specimen, there are also slight differences to the femur from Brunn, most notably in the position of the pneumatic foramen, which is more proximally placed in SNSB-BSPG 1977 XIX 39 (Textfig. 19). If these differences may indicate species differences or fall within the normal variation within *Ardeadactylus longicollum* will have to be shown in a revision of this genus.

5. Conclusions and outlook

The locality of Brunn has yielded a diverse and, at least in parts, excellently preserved vertebrate fauna

that is currently dominated by actinopterygian fishes, most notably teleosts. The aquatic fauna shows remarkable similarities to other known Kimmeridgian localities from the Late Jurassic carbonate platform along the northern rim of the Tethys. Especially noteworthy is that there might be greater similarity of this fauna to the fish fauna from the Kimmeridgian of Cerin than to the Tithonian faunas of the Solnhofen Archipelago, indicating that stratigraphic differences in faunas might be more marked than geographic and maybe (at least up to a certain level) ecological differences. Especially the terrestrial reptiles, mainly represented by rhynchocephalians, furthermore show a high degree of endemism. This might be due to island speciation (Losos & Ricklefs 2009), in which rhynchocephalian faunas rapidly diversified after dispersal over the different islands of the Solnhofen Archipelago, as it has often been interpreted in Recent lizards species (e.g. Glor et al. 2005). However, rapid replacement of lepidosaurian faunas over geological time can also currently not be ruled out.

The exceptional richness of the locality Brunn in combination with the excellent stratigraphic control of the finds (i.e. that each specimen can be exactly placed within the different Plattenkalk layers) provide an exceptional opportunity to study the dynamics of the early stages of faunal evolution in the Solnhofen Archipelago. Furthermore, some layers have only been recently explored, such as the plattenkalk layer 2, which has yielded the exceptionally preserved rhynchocephalian specimens and thus shows great potential for other terrestrial components of the fauna, so important new discoveries from this locality are more than likely. Thus, further exploration of the locality of Brunn, as well as in-depth studies of the remains that have already been retrieved will certainly result in important new insights into the origin of the Late Jurassic vertebrate faunas of southern Bavaria and their relation to other Late Jurassic faunas.

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Autor(en)/Author(s): Rauhut Oliver W. M., Lopez-Arbarelllo Adriana, Röper Martin, Rothgaenger Monika

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