Swiss J Geosci (2011) 104 (Suppl 1):S133–S146
DOI 10.1007/s00015-011-0061-5

# The fish fauna of the Late Jurassic Solothurn Turtle Limestone (NW Switzerland)

**Moyna K. Müller**

Received: 31 October 2009 / Accepted: 8 November 2010 / Published online: 28 June 2011

**Abstract** The surroundings of Solothurn (NW Switzerland) have been known for their fossil marine turtles since the beginning of the nineteenth century. In more recent history, access to the fossil bearing layers i.e. the *Rätschenbank* (Kimmeridgian, Late Jurassic) has not been possible until 1986 when one of the old quarries in the area re-opened. A series of excavations from 1986 to 1989 provided new material and a unique opportunity to re-investigate the fish fauna of the Solothurn Turtle Limestone that has not been dealt with since Agassiz (1833–1844). Examination and classification of the Solothurn specimens, mainly jaw fragments and teeth, furnished 11 species in 6 major groups: chimaeras (*Ischyodus*), selachians (*Hybodus*, *Paracestracion*, *Asteracanthus*), semionotids (*Lepidotes*), pycnodontids (*Gyrodus*, *Proscinetes*), caturids and oligopleurids (*Caturus*, *Callopterus*, *Ionoscopus*), and aspidorhynchids (*Belonostomus*).

**Keywords** Fish fauna · Palaeoecology · Microvertebrates · Late Jurassic · Solothurn Turtle Limestone · Jura Mountains · Switzerland

## Institutional abbreviations

NMS Naturmuseum Solothurn, Switzerland

## Introduction

The surroundings of Solothurn (NW Switzerland) have been known for their fossil marine turtles since the beginning of the nineteenth century. Well known were also fossil remains of other reptiles, fish and invertebrates (Lang and Rütimeyer 1867; Rütimeyer 1873; von Huene 1926; Bräm 1965; Thalmann 1966). More recently, this area has also made headlines with the discovery and description of large sauropod trackways (Meyer 1990, 1993). Historically, the Solothurn Turtle Limestone was quarried for building-stone thus providing access to the main fossil bearing layers until economic difficulties in the early 1920s forced the closure of all the region's 13 quarries (Meyer 1989, 1994b). Although the Solothurn Turtle Limestone produced the largest collection of Late Jurassic marine turtles worldwide, no further investigations into the genesis of this fossil site was possible until the re-opening of one of the old local quarries presented the opportunity to conduct excavations using modern palaeontological methods (Meyer 1988a, b, 1994b). In consequence, a series of excavations was undertaken from 1986 to 1989 in the main fossil-producing horizon, the *Rätschenbank* (Meyer 1994b). The objective of the project focused mainly on the analysis of the depositional environment and palaeoecology (Meyer 1988a) but also presented the opportunity to direct attention to the fish fauna of the Solothurn Turtle Limestone, which has not been dealt with since Agassiz (1833–1844) and thus providing further insight into ecological and taphonomical questions.

## Geographical and geological setting

The quarry of St. Niklaus (Gem. Rüttenen, Coord. 607.725/230.180) lies just north of the town Solothurn and

Editorial handling: Daniel Marty.

M. K. Müller (✉)
Department of Geology, University of Otago, 360 Leith Walk,
PO Box 56, Dunedin, New Zealand
e-mail: moyna.muller@stonebow.otago.ac.nz

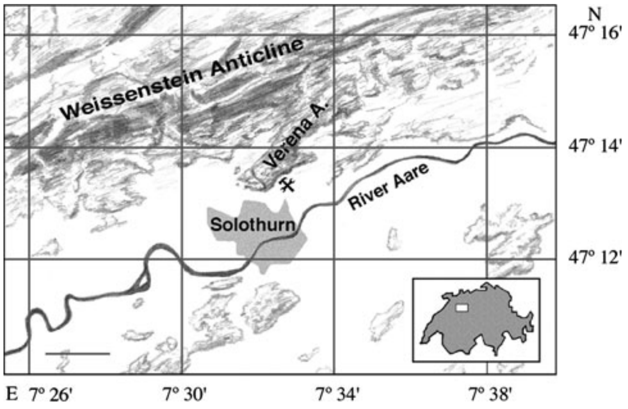

**Fig. 1** Relief of the Weissenstein and Verena Anticline in relation to the Quarry at St. Niklaus (⚒) near Solothurn. *Scale bar* 2 km

approximately 150 m northeast of the type locality Bieberstein (Fig. 1). Both quarries are situated within the Verena-anticline that surfaces about 10 km to the south of the main folds of the Jurassic range (Meyer 1988a, 1989, 1994b). In the St. Nicklaus quarry, the entire sequence of the Solothurn Turtle Limestone is exposed and has a thickness of 4–6 m (Meyer 1989).

The Solothurn Turtle Limestone forms the uppermost member of the Reuchenette Formation (Kimmeridgian, Late Jurassic) and has been defined by Meyer and Jordan (2000) as 'all layers above the *Halbwilde Bank*' and 'below the thinly layered Portland Limestone'. In the St. Niklaus quarry, the status of the *Kalkbänke* (Fig. 2) is not entirely clear, a preliminary examination, however, suggests that they are part of the lower Twannbach Formation, pending further investigations (Meyer pers. comm. 2008). The strata have a slight inclination to the south and locally exhibit small discontinuities (Meyer 1988a, 1994b). They predominantly consist of Mud- to Wackestones (Meyer 1994b).

At the excavation site, the main fossil-bearing horizon (*Hauptfundschicht*), the *Rätschenbank*, has a thickness of about 90 cm and is coped between the *Vierschühigen Bank* above and the underlying *Milde Bank* below (Meyer 1988a, 1989; Meyer and Jordan 2000).

## Stratigraphy and depositional environment

Sedimentological and stratigraphical analyses reveal that the entire Reuchenette Formation was deposited in a shallow marine to tidal flat setting covering large areas of northwestern Switzerland during the Late Jurassic (Meyer 1989; Colombié 2002; Jank et al. 2006a, b; Strasser 2007; Waite 2010). Algae and nerineid gastropods in the upper and lowermost banks exposed in the St. Niklaus quarry were deposited in higher subtidal to intertidal zones, whereas the middle part was influenced by slightly deeper subtidal water levels comprising echinoderm—stromboid gastropod or echinoderm—brachiopod communities (Meyer 1994b).

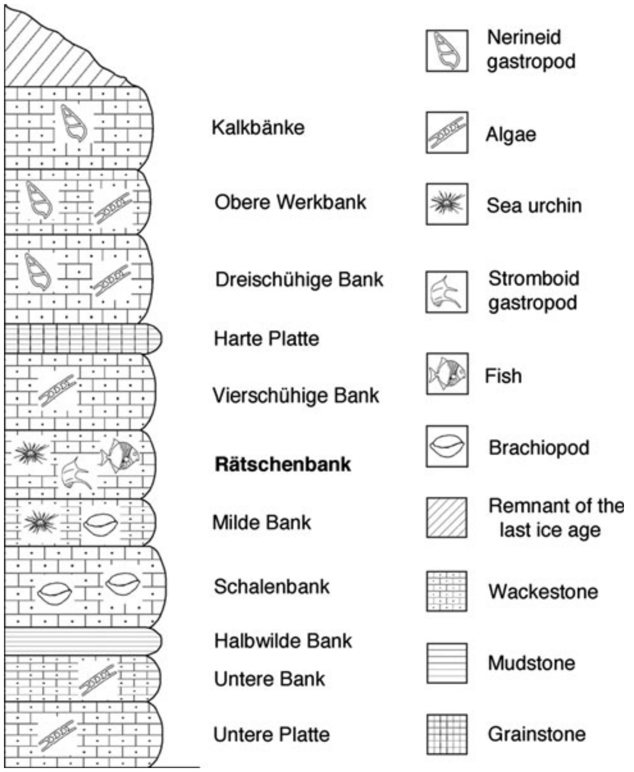

**Fig. 2** Schematical section of the St. Niklaus quarry. (After Meyer 1988a, 1994a, b)

The *Rätschenbank*, being part of this domain, was also influenced by deeper water levels. Sedimentological and palaeontological data suggest a deposition in a shallow, partly protected and well-oxygenated subtidal lagoon (Meyer 1988a). The *Rätschenbank*'s base reveals a fauna dominated by stromboid gastropods whereas the middle and particularly the upper part of the bank were exposed to increased eutrophic conditions as indicated by the abundance of sea urchins dependent on increased algae growth (Meyer 1994b; Meyer and Jordan 2000). The overall sedimentation rate was probably low but interrupted by rapid burial events caused by storms (Meyer 1988a, 1994b). Geological and palaeoecological observations in this area indicate a shallow, subtidal lagoon protected to the southeast by sandbars yet maintaining connections to the open sea towards the southwest (Meyer 1988a, 1989).

## Materials and methods

Five excavations from 1986 to 1989 targeted an area of about 250 $m^2$ excavating approximately a volume of

225 m$^3$ of the about 90 cm deep fossil-bearing layer, the *Rätschenbank* (Meyer 1989, 1994b). Excavation procedures were based on modern palaeoecological methods using a grid subdividing the excavation area into units of 1 m$^2$ and recording location, three-dimensional orientation and (in elongated fossils) declination to the north (Meyer 1988a, 1994b).

Initial examination of the stored material produced 857 promising specimens of which 469 came into closer consideration. After partial preparation, a preliminary identification reduced this number to 169 specimens. Of these, 85 specimens were prepared within the scope of the National Research Foundation Project. Preparation methods were mechanical with pneumatic chisels or chemical with formic acid. Fragile objects were strengthened using a dispersion of acrylic resin (Meyer 1988a, 1989). The other 84 specimens were prepared mechanically with pneumatic chisels and needles by the author. A final and more in-depth assessment resulted in the selection of 115 specimens that were photographed using cameras fitted with macro-zoom lenses. All photographed specimens were filed on computer by excavation number. After examination they returned to the Naturmuseum Solothurn for final storage. Subsequently those specimens received new inventory numbers recognizable by their prefix NMS (Naturmuseum Solothurn). Please note, specimens cited in this article refer to the inventory numbers of the Museum and not to the original excavation numbers. For a catalogue of all investigated and photographed specimens see Table 1.

## Systematic palaeontology

### Chimaeriformes

| | |
|---|---|
| Class | Chondrichthyes Huxley 1880 |
| Subclass | *Holocephali Bonaparte 1832* |
| Order | Chimaeriformes Patterson 1965 |
| Family | Chimaeridae Woodward 1891 |
| Genus | *Ischyodus* Egerton 1843 |
| Type species | *Chimaera townsendii* Agassiz in Buckland 1835 |

#### *Ischyodus sp. (NMS 20406 and NMS 20407)*

There are two jaw fragments that represent chimaeras in the Solothurn fish fauna. Structural indicative features in the chimaerean tooth plates are patches of hypermineralized tritorial tissue supported by a framework of trabecular dentine (Stahl and Chatterjee 1999). Number, shape, size and location of the tritorial tissue is diagnostic (Stahl and Chatterjee 1999). The first Solothurn specimen (NMS 20406, Fig. 3a) is a fragment of a left mandibular tooth plate. Although anteriorly and posteriorly broken, the parallel margins of the symphysial facet, indicative for *Ischyodus* (Egerton 1847), are still recognizable. Judged against a 28 cm long fossil of *Ischydous avitus* in Eichstätt (Germany) the Solothurn jaw fragment would indicate a total body length of about twice the size of the Eichstätt chimaera. The second specimen from Solothurn (NMS 20407, Fig. 3b) is an incomplete left palatine tooth plate. Extent and arrangement of the four tritorial surfaces are clearly recognizable and similar to those of *Ischyodus egertoni* Buckland, 1835 as figured by Duffin (2001) but the fragmentary nature of the specimen makes an unambiguous identification difficult. Additionally, reconstructed to its full size this animal would be approximately three times smaller than the other Solothurn specimen and obviously not originate from the same individual.

### Hybodontiformes

| | |
|---|---|
| Class | Chondrichthyes Huxley 1880 |
| Subclass | *Elasmobranchii Bonaparte 1838* |
| Order | Hybodontiformes *Patterson* 1966 |
| Superfamily | Hybodontoidea *Owen* 1846 |

#### *Hybodontiformes indet. (NMS 20409)*

Apart from teeth, there is also a specimen in Solothurn (NMS 20409, Fig. 3g) that may be part of a hybodont cranium. The fragment is about 50 mm wide by 60 mm long and recognizable by the typical hexagonal cartilaginous structures that are not present in bone. The remarkable preservation of the specimen is due to a slight calcification of the cartilage during the lifetime. The roughly triangular and badly fractured fragment consists mainly of deep cavernous cartilage with a smooth, slightly concave surface stepping down to a ledge on its outer border. This is a shape more likely to be associated with parts of the cranial structure rather than the generally flat or elongated elements of the postcranial skeleton. Overall the specimen cannot be identified accurately but, by way of elimination, it may be regarded as part of a selachian rostrum and taking its size and sturdy built into consideration, quite possibly of *Hybodus*.

#### *Hybodontoidea incertae sedis (NMS 20424)*

One of the most intriguing hybodont shark teeth of Solothurn is specimen NMS 20424 (Fig. 3c) superficially resembling the holotype of *Lissodus curvidens* described by Duffin and Thies (1977). The tooth is mesio-distally elongated and about 14.5 mm long. The tip of the central

**Table 1** Catalogue of all investigated and photographed specimens

| Inventory number | Classification | Description | Origin |
|---|---|---|---|
| NMS 7492[a] | *Lepidotes laevis* | Jaw fragment | Hist. |
| NMS 8160[a] | *Gyrodus jurassicus* | Lower jaw | Hist. |
| NMS 20406[b] | *Ischyodus* sp. | Left mandibular dental plate | 86-89 |
| NMS 20407[b] | *Ischyodus* sp. | Left palatine dental plate | 86-89 |
| NMS 20409[b] | Hybodontiformes indet. | Fragment of ?cranium | 86-89 |
| NMS 20410[a] | Heterodontiformes indet. | Calcified vertebra | 86-89 |
| NMS 20411, 20412, 20413[b] | *Paracestracion* sp. | Grinding tooth | 86-89 |
| NMS 20414[b] | *Asteracanthus* sp. | Grinding tooth | 86-89 |
| NMS 20415, 20416, 20417[b], 20419 | *Hybodus* sp. 1 | Multicuspid tooth | 86-89 |
| NMS 20418, 20420, 20421[b], 20422 | *Hybodus* sp. 2 | Multicuspid tooth | 86-89 |
| NMS 20423[b] | Heterodontiformes indet. | Fragment of tooth cusp | 86-89 |
| NMS 20424[b] | Hybodontoidea incerta sedis | Multicuspid tooth | 86-89 |
| NMS 20425, 20426[b], 20427[b], 20428–20433 | *Lepidotes* sp. | Grinding tooth or enameloid cap | 86-89 |
| NMS 20434–20436 | *Proscinetes* sp. 2 | Enameloid cap of grinding tooth | 86-89 |
| NMS 20438[b] | Pycnodontiformes indet. | Enameloid cap of grinding tooth | 86-89 |
| NMS 20439–20441, 20442[b] | *Gyrodus* sp. | Incisor | 86-89 |
| NMS 20443–20452 | *Proscinetes* sp. 1 | Enameloid cap of grinding tooth | 86-89 |
| NMS 20453, 20454[b], 20455[b], 20456–20457, 20458[b], 20459–20460 | *Proscinetes* sp. 1 | Vomer | 86-89 |
| NMS 20461[b] | *Proscinetes* sp. 2 | Vomer | 86-89 |
| NMS 20462[b] | Pycnodontiformes indet. | Vomer | 86-89 |
| NMS 20463–20467, 20468[b], 20469[b], 20470–20475 | *Proscinetes* sp. 1 | Prearticular | |
| NMS 20476, 20477[b], 20478–20484 | *Proscinetes* sp. 2 | Prearticular | 86-89 |
| NMS 20485[b], 20486–20495, 20497, 20499–20500, 20502–20509, 20510[b], 20511–20512 | *Caturus* sp. | Fang | 86-89 |
| NMS 20496, 20498, 20501, 20515[a] | Halecomorphi indet. | Fang | 86-89 |
| NMS 20513[b] | *Callopterus* sp. | Fang | 86-89 |
| NMS 20514[b] | *Ionoscopus* sp. | Fang | 86-89 |
| NMS 20516[b] | *Belonostomus* sp. | Predentary | 86-89 |
| NMS 20517[b] | Osteichthyes indet. | Left lower jaw | 86-89 |
| NMS 20518[b] | Halecomorphi indet. | Right cleithrum | 86-89 |
| NMS 20519[a] | Semionotidae indet. | Scale | 86-89 |
| NMS 20520[a], 20521[a] | Halecomorphi indet. | Scale | 86-89 |

These excavations were initially undertaken by the Naturmuseum Solothurn (winter 1986) and continued by the Geological Institute of the University of Bern (summers 1986–1989)

*NMS* Naturmuseum Solothurn, *Hist.* Historical collection of the NMS, *86-89* specimens originating from the 1986–1989 excavations in the quarry of St. Niklaus

[a] Specimen cited but not figured in this article

[b] Specimen cited and figured in this article

cusp, large areas of the distal side and most of the root are missing. Flanking the central cusp are three distinctively smaller lateral cusplets that do not decrease in size laterally. Well-defined vertical striae extend labially and lingually over both the central cusp and the lateral cusplets. There is a row of unusually large labial nodes fronting the central and lateral cusps. The labial nodes are separated by deep furrows from each other and from the labial surface of the crown. They do not decrease in size mesiodistally as in the specimen described in Duffin and Thies (1977). The

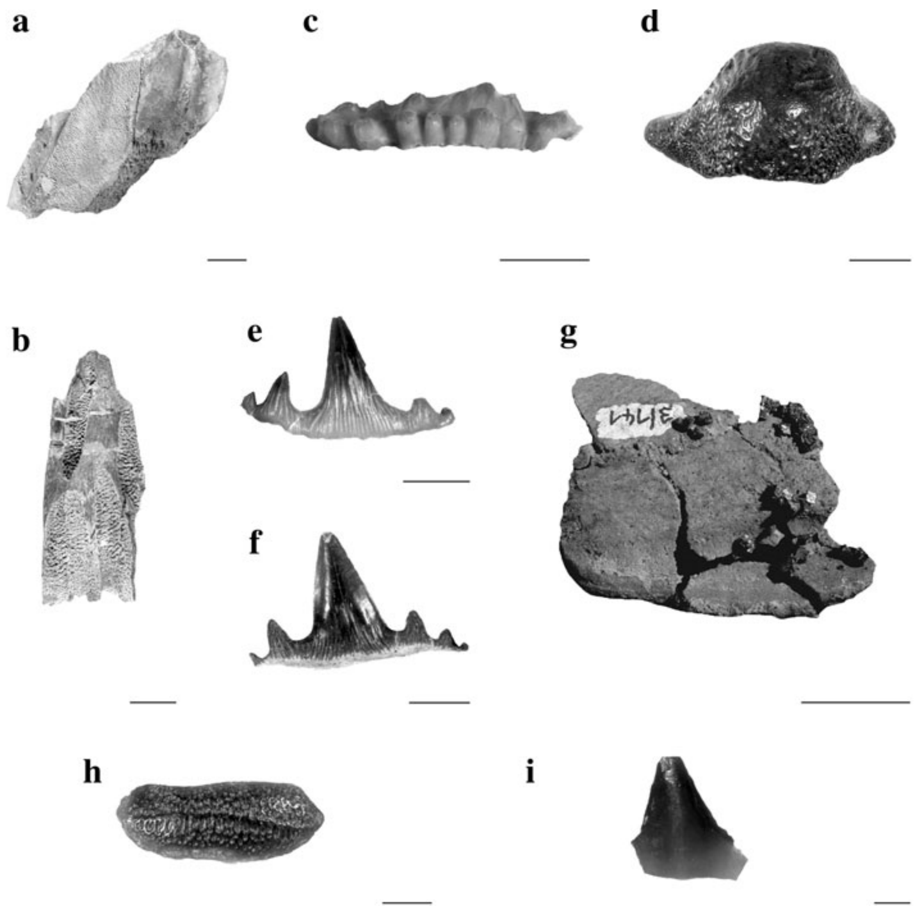

**Fig. 3** **a**, **b** Chimaeras, *Ischyodus* sp. **a** NMS 20406, fragment of left mandibular tooth plate, occlusal view. **b** NMS 20407, incomplete left palatine tooth plate, occlusal view. **c–i** Sharks. **c** NMS 20424, Hybodontoidea incerta sedis, labial view. **d** NMS 20414, *Asteracanthus* sp., oblique occlusal view. **e** NMS 20417, *Hybodus* sp. 1, labial view. **f** NMS 20421, *Hybodus* sp. 2, labial view. **g** NMS 20409, Hybodontiformes indet., possible fragment of a cranium. **h** NMS 20413, *Paracestracion* sp., occlusal view. **i** NMS 20423, Heterodontiformes indet., labial view. *Scale bars* 2.0 cm (**g**), 1.0 cm (**a**), 0.5 cm (**b**–**f**), 0.1 cm (**h**, **i**)

occlusal crest is narrow and sharp. At first sight the tooth strongly reminds of teeth belonging to *Lissodus* sp. or *Polyacrodus* sp. The labial nodes have been used in the past as diagnostic character to distinguish between *Polyacrodus* and *Hybodus* (Rees and Underwood 2002), but are also present in *Lissodus*, *Lonchidion* and up to a certain degree in *Parvodus* (Rees and Underwood 2002). It is difficult to assign the Solothurn specimen to any of these genera, more so as the status of *Polyacrodus* still remains to be re-evaluated (Rees and Underwood 2002). Furthermore *Polyacrodus* teeth cannot be diagnosed on dental morphology alone and should preferably be referred to as *Hybodus* (Rees 2008). Other complications also arise by the presence of various tooth morphotypes within one species (Duncan 2004) and the incomplete preservation and unusual presence of a row of uni-sized labial nodes in the Solothurn specimen. One of the most striking characteristics of this tooth however is its size: whereas teeth of *Lissodus*, *Lonichidion* and *Parvodus* usually remain within a range of a few millimeters (Rees and Underwood 2002; Duncan 2004) the Solothurn specimen, if complete, would measure about 19 mm in length, a tooth size much more associated with *Hybodus*.

### *Hybodus*

| | |
|---|---|
| Family | Hybodontidae Owen 1846 |
| Genus | *Hybodus* Agassiz 1837 |
| Type species | *Hybodus reticulatus* Agassiz 1837 |

The genus *Hybodus* encompasses a heterogeneous assembly of specimens and is in urgent need of a taxonomic revision (Rees and Underwood 2002). Until this is done, the specimens described here will remain in the genus *Hybodus*. From the Solothurn excavation a total of eight teeth have been recovered. They display a broad, labiolingually moderately compressed central cusp surpassing at least 2 or 3 well-separated lateral cusplets (except in one incomplete specimen where only one cusplet remained attached to the central cusp). All teeth are well preserved but show wear and tear marks confined to the apex of the central cusp or breakages between the lateral cusplets. It is not possible to determine if these breakages occurred due to mechanical stress when feeding, taphonomically or as a result of the excavation. The Solothurn specimens show a variety of features comparable to four tooth fragments of *Hybodus* sp. 2 from the Kimmeridgian of Ringstead that have been described by Underwood (2002). Underwood compares *Hybodus* sp. 2 to the British Wealden shark *H. ensis* Woodward, 1916 noting as the main difference the coarser striae on the lateral cusplets of *Hybodus* sp. 2. In this respect the Solothurn specimens seem to match Underwood's *Hybodus* sp. 2, although both the Ringstead specimen and some of the Solothurn specimens appear to feature overall coarser striae than *H. ensis* Woodward, 1916. Furthermore, *H. ensis* was described by Patterson (1966) as only having one pair (or rarely a second minute pair) of lateral cusplets. Similarly Underwood observed that the tooth fragments of *Hybodus* sp. 2 had at least one pair of lateral cusplets but gives no indication of numbers in a hypothetical complete tooth. On the other hand, the Solothurn specimens appear to bear three pairs of lateral cusplets if fully reconstructed and would therefore match neither. In 2008 Rees and Underwood consigned *H. ensis* Woodward, 1916 to a new genus, *Planohybodus*, including two additional species, *P. peterboroughensis* and *P. grossiconus* from the English Bathonian and Callovian, respectively (Rees and Underwood 2008). They note that all three species are very similar yet can be easily recognized by the presence of one (*P. ensis*), two (*P. grossiconus*) or three (*P. peterboroughensis*) pairs of lateral cusplets in the upper anterior teeth. In this respect, the Solothurn specimens superficially match *P. peterboroughensis* but lack the small nodules at the basal end of the striae or the broad bridge between the main cusp and lateral cusplets. Furthermore, the Solothurn specimens can be divided into two morphological groups defined by the characteristics of the striae and the contour of the central cusp. Whether this is a reflection of true species diversity cannot be ascertained but the two morphological groups are here referred to as *Hybodus* sp. 1 and *Hybodus* sp. 2. Note that the two morphological groups *Hybodus* sp. 1 and sp. 2 discussed in this work are not the same as *Hybodus* sp. 1 and 2 of Underwood (2002) and should therefore not be confused with the latter.

### *Hybodus sp. 1 (NMS 20415–20417, NMS 20419)*

The teeth of *Hybodus* sp. 1 (e.g. NMS 20417, Fig. 3e) are characterised by a slender central cusp gradually tapering towards the tip, flanked on both sides by a straight cutting edge. The ratio of cusp height/width at midpoint is about 4.0. Lingually, the central cusp follows a more pronounced sigmoidal curvature. The striae are coarser than those of *Hybodus* sp. 2 and cover about 2/3 of the labial face on the central cusp respectively reach the tip of the inner lateral cusplets. The outermost lateral cusplets have been broken off on specimen NMS 20417 but other, more complete specimens from Solothurn reveal a third, albeit minute lateral pair of cusplets.

### *Hybodus sp. 2 (NMS 20418, NMS 20420–20422)*

The teeth of *Hybodus* sp. 2 (e.g. NMS 20421, Fig. 3f) present a prominently broad central cusp that is lingually only slightly arched. The two faces are divided by a faintly sigmoid but labially displaced cutting edge. The ratio of cusp height/width at mid point is about 2.9. The striation of the enameloid is fine and remains labially constrained to the lower third of the central cusp. On the inner pair of lateral cusplets the striae extend 3/4 upwards of the labial face not quite reaching the tip.

Although both *Hybodus* species 1 and 2 from Solothurn resemble teeth described by Patterson (1966), Underwood (2002) and Rees and Underwood (2008) in morphology and approximate size, a precise identification of the Solothurn specimens *Hybodus* sp. 1 and 2 is complicated by wear and tear marks, breakages and the low number of teeth recovered. Further questions also arise considering the incongruency of age and origin of the Solothurn fossils when compared to the British Middle Jurassic and Wealden specimens.

### *Asteracanthus sp. (NMS 20414)*

| | |
|---|---|
| Family | Acrodontidae Casier 1959 |
| Genus | *Asteracanthus* Agassiz 1837 |
| Type species | *Asteracanthus ornatissimus* Agassiz 1837 |

*Asteracanthus* is represented only by one tooth (NMS 20414, Fig. 3d). Teeth of this genus are characterised by a grinding-type dentition with a tendency to monognathic heterodonty (Cappetta 1987). The Solothurn specimen is a large, massive tooth that is relatively little expanded transversely. The crown is centrally high and globular, and marginally lower and narrower with a slight lateral crest protracting into two points. In occlusal view the tooth approaches a labially slightly displaced hexagonal shape. The mostly broken enameloid/root-boundary suggests a sinuous curvature, the root is entirely missing. The top of the crown shows signs of strong abrasion but retains a reticulate enameloid pattern in the lower circumference. The hexagonal contour, laterally still visible occlusal crest, domed centre and weakly arched crown base together with the reticulate ornamentation of the crown fits well within the diagnosis of anterior teeth of *Asteracanthus medius* from the English Bathonian and Callovian (Peyer 1946; Rees and Underwood 2008). However, the strong coronal abrasion of the crown and the important difference in age make an unambiguous identification at species level difficult and the tooth is therefore assigned to *Asteracanthus* sp.

## Heterodontiformes

| | |
|---|---|
| Class | Chondrichthyes Huxley 1880 |
| Subclass | *Elasmobranchii Bonaparte 1838* |
| Order | Heterodontiformes Berg 1940 |

### *Heterodontiformes indet. (NMS 20410, NMS 20423)*

A fragment of a tooth cusp (NMS 20423, Fig. 3i) and a calcified vertebra (NMS 20410, not figured) of a neoselachian shark or ray are both too indistinct to be identified precisely even so they fit well within the size range of *Paracestracion*, the only confirmed neoselachian shark in Solothurn. In specimen NMS 20423 merely the top of the central tooth blade is preserved, the lateral cusplets, large portions of the lingual face including the apron and the root are entirely missing making a definite identification impossible.

### *Paracestracion sp. (NMS 20411–20413)*

| | |
|---|---|
| Family | Heterodontidae Gray 1851 |
| Genus | *Paracestracion* Koken in Zittel 1911 |
| Type species | *Cestracion falcifer* Wagner 1857 |

Based on dental characteristics, fossil heterodontid teeth have been included for a long time into the genus *Heterodontus*. However, there are important differences between extant *Heterodontus* and Late Jurassic *Paracestracion* species, a fact that has only recently found wider acceptance (Kriwet and Klug 2004). There are three molariform teeth of *Paracestracion* (e.g. NMS 20413, Fig. 3h) in the Solothurn assemblage. The oral face of the crown is slightly domed and rectangular, parallelogram or lenticular in shape. It shows the characteristic labially reticulate and lingually striate bifurcating ornamentation separated by a transverse median fusion line if not too worn. The root is lower and narrower than the crown. The transverse median fusion line (called 'transverse crest' by Cappetta 1987), ornamentation of the enameloid cap and morphology of the tooth-root are characteristic features of heterodontids (Kriwet and Klug 2004).

## Semionotiformes

| | |
|---|---|
| Class | Osteichthyes Huxley 1880 |
| Subclass | Actinopterygii Cope 1887 |
| Infraclass | Neopterygii Regan 1923 |
| Order | Semionotiformes *sensu* Olsen and McCune 1991 |
| Family | Semionotidae Woodward 1890 |
| Genus | *Lepidotes* Agassiz 1832 |
| Type-species | *Lepidotes elvensis* (Blainville 1818) |

### *Lepidotes sp. (NMS 20425–20433)*

The last series of excavations mostly uncovered scales and teeth. However, there is also a tooth bearing part of the jaw in the museum's historical collection (NMS 7492, not figured). Teeth of *Lepidotes* are easily recognized by a sheath of enameloid that is not restricted to the crown but also envelops the upper part of the tooth neck like a collar and was thus referred to by J. Thomasset in 1930 as 'émail du collet' (Peyer 1954) and by Mudroch and Thies (1996) as 'Schmelzmanschette'. The domed crown is in most cases worn and the small central tubercle, typical for new, unused replacement teeth (Peyer 1954) (NMS 20427, Fig. 4a), hardly ever visible (e.g. NMS 20426, Fig. 4b). There is a total of nine well-preserved teeth showing distinctive wear and tear patterns that have developed during the lifetime of the animal and not by mechanical abrasion in a current. Although there are differences in tooth morphology at species level, a reliable diagnostic is not possible based on a tooth alone. Also recovered were a number of rhombic ganoid scales including one particularly well-preserved scale of just over 10 mm (NMS 20519, not figured). Size and shape of this scale correspond well with that of a larger semionotid, most likely *Lepidotes*.

## Pycnodontiformes

| | |
|---|---|
| Class | Osteichthyes Huxley 1880 |
| Subclass | Actinopterygii Cope 1887 |
| Infraclass | Neopterygii Regan 1923 |
| Order | Pycnodontiformes Berg 1937 |
| Family | Pycnodontidae Agassiz 1833 *sensu* Nursall 1996 |

Most of the fossil remains of pycnodonts are represented by teeth, palates, jaw fragments and near complete hemimandibles. Isolated teeth are mostly represented by crushing teeth of the palate or the lower jaw. Divergent to *Lepidotes* pycnodonts do not have a 'Schmelzmanschette'. As a result, the enameloid cap may part easier from the neck of the tooth and may not show any signs of breakage. On the other hand, teeth in the jaw may lack the enameloid cap entirely, merely revealing the remaining tooth necks deeply embedded in the bone cement. Pulp cavities in the centre of the tooth often remain devoid of sediment, giving the protruding tooth necks the look of small chimneys. The lack of sediment indicates that the enameloid cap may have parted from the tooth neck after fossilization. In some cases, the enameloid cap has been ground down to the tooth neck but without separating; the bond though is then very feeble and enameloid caps often have to be glued back on after preparation.

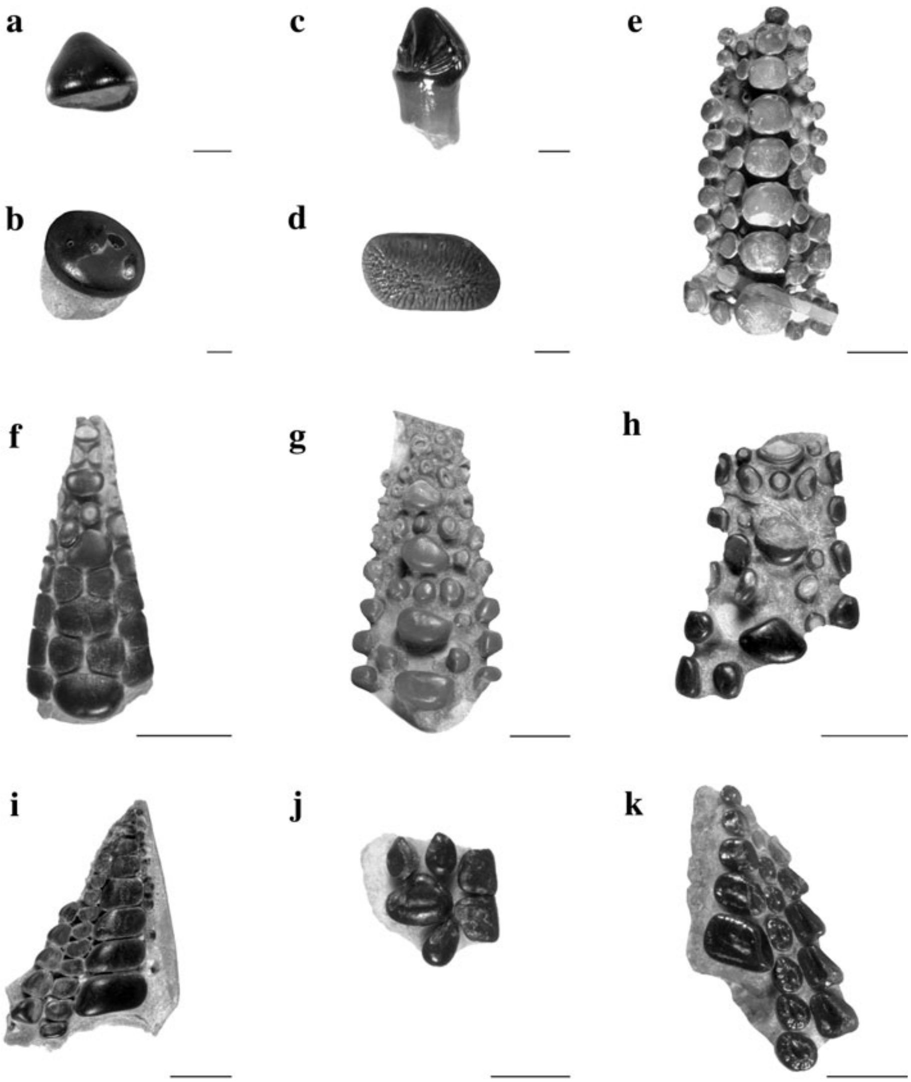

**Fig. 4** **a**, **b** Semionotid teeth, *Lepidotes* sp. **a** NMS 20427, view from oblique blow. **b** NMS 20426, view from oblique above. **c**–**k** Pycnodont jaws and teeth. **c** NMS 20442, *Gyrodus* sp., incisor, oblique lingual view. **d**–**e** Pycnodontiformes indet. **d** NMS 20438, enameloid cap, occlusal view. **e** NMS 20462, vomer, occlusal view. **f**–**i** *Proscinetes* sp. 1. **f** NMS 20455, vomer, MT 1, occlusal view. **g** NMS 20454, vomer MT 2, occlusal view. **h** NMS 20458, vomer, MT 3, occlusal view. **i** NMS 20468, left prearticular, occlusal view. **j**–**k** *Proscinetes* sp. 2. **j** NMS 20461, fragment of vomer, occlusal view. **k** NMS 20477, right prearticular, occlusal view. *Scale bars* 1.0 cm (**e**), 0.5 cm (**b**, **c**, **f**–**k**), 0.1 cm (**a**, **d**)

### *Terminology and general description of dental arrangement*

Contrary to earlier suggestions mentioned by Kriwet (2004) pycnodont fishes probably had more than a single generation of teeth. As stated by Longbottom in 1984, both Woodward (1895) and Thurmond (1974) suggested that pycnodont dentitions grew by addition of larger teeth at the posterior end of the vomer or prearticular, a view Longbottom revised and extended. She supports her findings with material comprising Tertiary pycnodont dentition from Mali. She confirms the hitherto well-known regular dental arrangement in rows but also describes an additional multitude of small, circular and irregularly arranged anterior teeth she finds present only in adult specimens. This and the distinctive wear pattern that is only prominent on the front of the regular tooth rows, leads her to conclude that the pycnodont dental pattern is not determined by substitution but by posterior and anterior additional tooth growth. On the other hand, Poyato-Ariza and Wenz (2005) discovered in a specimen of *Akromystax* two deeply in the bone embedded teeth. Both teeth were found far away from the occlusal surface and in a position of about a 90° angle. This finding is also in accordance with Peyers (1954) description of tooth replacement in *Lepidotes*. Poyato-Ariza and Wenz deduced that occasional successional tooth replacement is possible in the lower jaw; a finding that is supported by various Solothurn specimens (prearticulars and vomers) where large indentations or smooth circular cavities in place of a tooth indicate tooth loss and possible later replacement (Fig. 5).

Functional–morphological characteristics of the upper and lower jaw are a direct reflection of the strong correlation between dentition efficiency and anatomical adaptations of the jaws and are exemplary demonstrated in the Solothurn pycnodonts. The significance of dental character sets as a systematic tool was investigated by Poyato-Ariza (2003). He concluded that they are

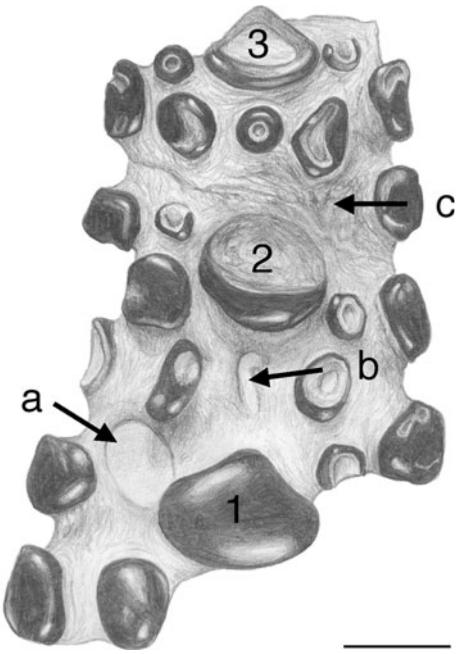

**Fig. 5** Tooth replacement. *Proscinetes* sp. 1, Morphotype 3, NMS 20458, vomer, occlusal view. Three longitudinal intercalated tooth rows form a transverse repetitive tooth-pattern of 2:3:2. 1 to 3, teeth of the main row, note increased wear from 1 to 3; *a* to *c*, signs of tooth loss. *a* oval cavity of recently lost tooth. *b* partly overgrown cavity. *c* scarred bone tissue from healed cavity. *Scale bar* 0.25 cm

indispensable to determine the interrelationship of the family Pycnodentidae but that they should be considered only as part of the total morphological evidence and not in isolation. This is an important aspect considering that the crushing dentition of pycnodonts is very durable and often the sole remnant of the fish. Diagnostic character sets may include vomerine and prearticular tooth arrangement (particularly when combined), number and relation of individual teeth and tooth rows to each other and morphological characteristics of individual teeth (Kriwet 2004; Poyato-Ariza and Wenz 2005).

In pycnodonts the tooth bearing elements of the upper jaw are composed of the vomer (unpaired palatine bone) and the premaxillae. In the Solothurn specimens the vomer supports the median (or main) tooth row that is formed by the largest molariform teeth and flanked on each side by one lateral row of smaller teeth (Fig. 6a). Intercalated between the median and the lateral rows are two or three additional tooth rows, a feature regarded as exclusive of *Proscinetes* (and *Neoproscinetes*, Poyato-Ariza and Wenz 2002). They form a characteristic repetitive transverse pattern (across the rows) subdividing *Proscinetes* sp. 1 into three distinct morphotypes (MT 1-3) that will be discussed in detail further below. The most anterior bone of the upper jaw, the premaxillary, generally supports two or three incisors arranged in one row (Poyato-Ariza and Wenz 2005). No premaxillary was found in Solothurn.

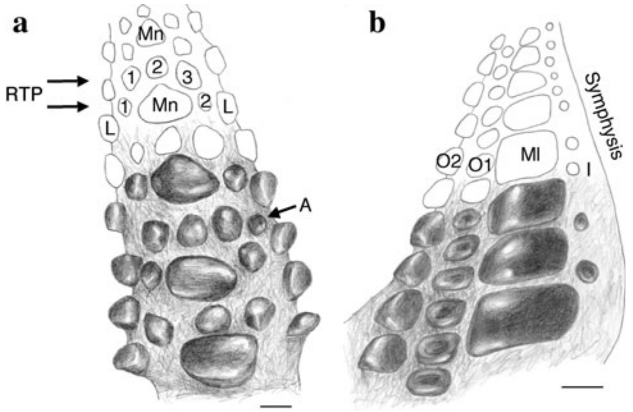

**Fig. 6** Dental arrangement. **a** Vomer, reconstructed Morphotype 2 based on specimen NMS 20454. **b** Prearticular, reconstruction based on specimen NMS 20468. *A* additional tooth, *I* inner tooth row, *L* lateral tooth row, *Ml* medial tooth row, *Mn* median tooth row, *O1 and O2* first and second outer lateral tooth row, *RTP* repetitive transverse pattern comprising *1–2* and *1–3* intercalated teeth. *Scale bars* 0.2 cm

The lower jaw comprises two paired tooth bearing elements: the large prearticular, sometimes referred to as splenial, and the dentary. The prearticular supports one medial (or main) tooth row, the largest molariform teeth in the lower jaw, and several smaller lateral rows. In the Solothurn specimens the medial row is flanked on its outer side by a first outer (proximate) and a second outermost (distal) lateral row of smaller teeth and mesially by one, often vaguely defined, inner lateral row of even smaller sized teeth (Fig. 6b). The dentary generally supports two or three incisors arranged in one row (Poyato-Ariza and Wenz 2005). However, no dentary has been found in the Solothurn assemblage.

In both the upper and the lower jaw, the main row forms a pillow like elevated occlusal surface rising above the lateral rows. The tooth size in all rows decreases anteriorly giving the jaw a pointed outline. Additionally, the two outer lateral rows also show a reduction of tooth diameter in labio-lingual direction.

The Solothurn specimens can generally be divided into two groups that can be distinguished by the presence, respectively, absence of ornamentation in the enameloid cap. Absence of ornamentation may sometimes be difficult to infer, particularly where the lack of ornamentation is clearly due to the abrasion of the crown. However, some specimens from Solothurn show little signs of wear and seem to naturally lack ornamentation.

### *Proscinetes* Gistl *1848*

### Subfamily Proscinetinae Gistl 1848

The most common specimens found in the Solothurn assemblage are jaws and teeth of *Proscinetes*. In vivo, the

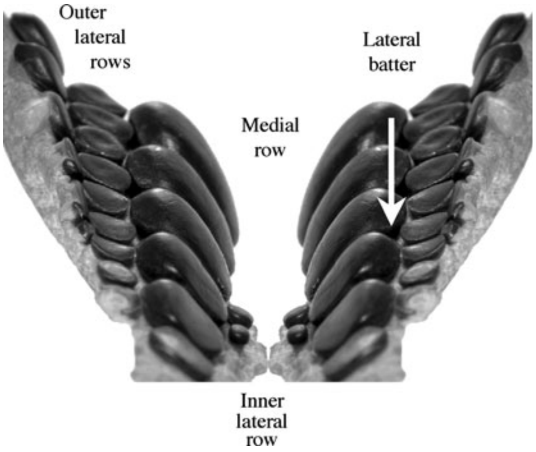

**Fig. 7** Spatial arrangement of the lower jaw. Mirrored images of specimen NMS 20469 illustrating the three dimensional arrangement of the two hemi-mandibles. *Frontal view* not to scale

two opposing medial rows in the lower jaw probably approached each other at a steep angle (Fig. 7). Furthermore, the overhanging bulge of each enamel cap created, in combination with its neighbour, a lateral batter along the flank of the tooth row. The outer lateral batter thus formed, in conjunction with the outer lateral tooth rows and the teeth of the other hemi-mandible, a U-shaped through jointly counteracting the upper jaw in the manner of a 'nutcracker' similar to that described of *Stemmatodus rhombus* by Kriwet (2004). In some specimens the teeth are extremely tightly packed and the bulging enameloid caps in close contact. Abrasion, grinding the initially domed enameloid surface down, may then create an almost compact and level surface that is supported by the slim tooth necks and the surrounding bone cement. In some cases, neighbouring teeth stand tightly enough to prevent a preparation needle half the diameter of a human hair to be inserted between two adjacent enameloid caps.

On the vomer the lateral row consists in some specimens of D-shaped, sometimes tightly packed enameloid caps where the outer edge of the teeth form a continuous line (e.g. NMS 20455, Fig. 4f and NMS 20461, Fig. 4j). The lateral row comprises roughly twice as much teeth as the median row. In the median row, the oval shaped enameloid caps may also take on anteriorly a novel triangular shape in which the two anterior edges appear slightly concave and the posterior edge convex (e.g. NMS 20454, Fig. 4g and NMS 20458, Figs. 4h, 5). There are two or three additional longitudinal rows intercalating beside or in between the median row forming a repetitive transverse pattern (RTP) of one (e.g. NMS 20455, Fig. 4f), two (e.g. NMS 20454, Figs. 4g, 6a) or three transversely orientated rows (NMS 20458, Figs. 4h, 5).

### *Proscinetes sp. 1 (Solitary teeth NMS 20443–20452, Vomers NMS 20453–20460, Prearticulars NMS 20463–20475)*

Ten solitary teeth, eight partially preserved vomers and 13 more or less complete prearticular hemi-mandibles were consigned to this group. Tooth crowns are not ornamented. The prearticular supports a medial row flanked by two medium-sized outer lateral rows and one rather small, loosely defined inner lateral row (e.g. NMS 20468, Fig. 4i). This small inner lateral row seems not to have been acknowledged by Poyato-Ariza and Wenz (2002) in their diagnosis for *Proscinetes*. Generally, the close arrangement of the teeth and pronounced decrease of the crown radius anteriorly, laterally and mesially produces a steep angle in the jaw line culminating in a pointed snout.

In occlusal view, the enameloidoid caps of the prearticular medial row are in most cases densely packed and take on an oblong to oblique-rectangular shape. In the lateral rows they are circular to oval shaped and sometimes feature a central notch that is not present in the vomer. The vomers include different specialization grades forming loosely- (e.g. NMS 20454, Figs. 4g, 6a) to densely-packed (e.g. NMS 20455, Fig. 4f) and slightly to highly symmetrical grinding dentitions. Overall three morphotypes (MT) can be distinguished: MT 1 with one intercalating transverse tooth row and a repetitive transverse pattern (RTP) of 2 (e.g. NMS 20455, Fig. 4f). MT 2 featuring two intercalating transverse tooth rows and a RTP of 2:3 (e.g. NMS 20454, Figs. 4g, 6a). MT 3 with three intercalating transverse tooth rows and a repetitive transverse pattern of 2:3:2 (NMS 20458, Figs. 4h, 5). The prearticulars do not encompass such a wide range of differentiation. Many of the jaws reveal clear signs of wear, particularly in areas of high stress. There is particularly in this group a tendency of the teeth in the anterior part of the jaw to be worn down significantly more than the teeth in the posterior part (e.g. NMS 20455 Fig. 4f or NMS 20454, Fig. 4g), a phenomenon that has been observed by various authors in the past (see also paragraph 'Terminology and general description of dental arrangement' above). The majority of jaws are estimated to be about 2 cm long suggesting an overall body size of approximately 30 cm. Nonetheless larger specimens amongst the twelve isolated enameloid caps imply significantly larger fish.

### *Proscinetes sp. 2 (Solitary teeth NMS 20434–20436, Vomer NMS 20461, Prearticulars NMS 20476–20484)*

One fragment of a vomer and nine partially-preserved prearticulars were allocated to the second group. They roughly match the tooth morphology and arrangement of the first group, but the enameloid caps clearly show, if not worn down, a central notch surrounded by a crenulated ridge chased radially with minute, densely aligned tubercles. In the prearticular the teeth of the outermost lateral row take on the shape of a rectangular triangle with the hypotenuse approaching the body axis at an angle of about 45° giving the jaw a fir-tree like look (e.g. NMS 20477, Fig. 4k). In the vomer, the outer edge of the D-shaped, tightly packed enameloid caps of the lateral row form an uninterrupted line. Oval to tear drop shaped teeth in the alternate rows completely intercalate in between the teeth of the median row (NMS 20461, Fig. 4j). As in the first group, the anterior tooth crowns of the median row in the vomer seem to have a tendency to take on a sub-triangular shape. The vomer and all prearticulars of this group are comparable in size with those of the first group. Amongst the four isolated enamel caps there are also some that may originate from larger fish.

### *Gyrodus sp. (NMS 20439–20442)*

| | |
|---|---|
| Family | Gyrodontidae Berg 1940 |
| Genus | *Gyrodus* Agassiz 1833 |
| Type species | *Stromateus hexagonus* Blainville 1818 |

No prearticulars of *Gyrodus* were found in the Solothurn excavation project, but a lower jaw housed in the historical collection of the museum (NMS 8160, not figured) can be referred to this species. The specimen comprises both hemi-mandibles of the lower jaw and is easily recognizable by the diagnostic dental key character, the typical central papilla, as defined by Poyato-Ariza and Wenz (2002). The excavation, however, produced four of the characteristic robust, hook-shaped incisors (e.g. NMS 20442, Fig. 4c). Some of these teeth are large enough to be associated with the larger gyrodont-type as described by Lambers (1992).

### *Pycnodontiformes indet. (NMS 20438, NMS 20462)*

Additional specimens found in Solothurn are a single isolated enameloid cap (NMS 20438, Fig. 4d) and a vomer (NMS 20462, Fig. 4e). The enameloid cap may be tentatively identified as *Eomesodon* or *Apomesodon*. *Eomesodon*, as understood for a long time, has represented an unnatural grouping and some specimens of this species have since been included in *Apomesodon* (Poyato-Ariza and Wenz 2002). The molariform tooth is distinguishable by a slight but highly dense, rugose pattern in the surface of the enameloid cap and by its grey (not black) appearance.

The second specimen, an almost entirely-preserved vomer, may be tentatively identified as *Macromesodon*, *Eomesodon or Apomesodon*. Besides the above-mentioned complications, classification of the vomer is further complicated by the lack of diagnostic dental character sets linked to these genera (Poyato-Ariza and Wenz 2002). The specimen reveals a loosely associated but distinct arrangement of five tooth rows comprising predominantly circular to subcircular teeth. All enameloid caps are smooth with little signs of wear and tear. The median tooth row comprises at least 7 teeth. Fully reconstructed the specimen would probably be about 6 cm long suggesting a fish of about 50 cm.

## Halecomorphi

| | |
|---|---|
| Subdivision | Halecomorphi Cope 1872 |
| Order | Amiiformes Hay 1929 |
| Suborder | Caturoidea Owen 1860 |
| Family | Caturidae Owen 1860 |
| Genus | *Caturus* Agassiz 1833 |
| Type species | *Caturus furcatus* Agassiz 1833 |

### *Caturus sp. (NMS 20485–20495, NMS 20497, NMS 20499–20500, NMS 20502–20512)*

The saggitate teeth of *Caturus*, *Ionoscopus* and *Callopterus* are fairly similar to each other (Mudroch and Thies 1996). However, in *Caturus* (e.g. NMS 20485, Fig. 8a and NMS 20510, Fig. 8b) the tooth-crown is flanked by characteristically pronounced, lingually displaced straight blades (Mudroch and Thies 1996). The cutting edges emerge at the top of the tooth as small, sharp ridges broadening towards the base of the enameloid cap and are sometimes encroaching on the upper part of the tooth neck forming a shank. The enameloid cap is lingually flattened, respectively, labially pronounced convex. In lateral view, the contour of the crown remains lingually straight but labially tends to take on a slight concave curvature from base to tip. This and the strong lingual curvature of the tooth neck give the tooth overall a slight sigmoidal appearance that is diagnostic for *Caturus* (Mudroch and Thies 1996). The majority of the teeth and tooth fragments found in Solothurn, over 40 in numbers, belong to *Caturus*. It is also the dominant predatory fish genus found in other locations such Langenberg in North Germany (Mudroch and Thies 1996).

### *Ionoscopus sp. (NMS 20514)*

| | |
|---|---|
| Order | Ionoscopiformes Grande and Bemis 1998 |
| Family | Ionoscopidae Lehman 1966 |
| Genus | *Ionoscopus* Costa 1853 |

Compared to *Caturus* the tooth neck of *Ionoscopus* is straighter and stouter. The two cutting edges of the lingually curved enameloid cap are less prominent and not straight as in *Caturus* but slightly arched (Mudroch and Thies 1996). One tooth was found to clearly belong to

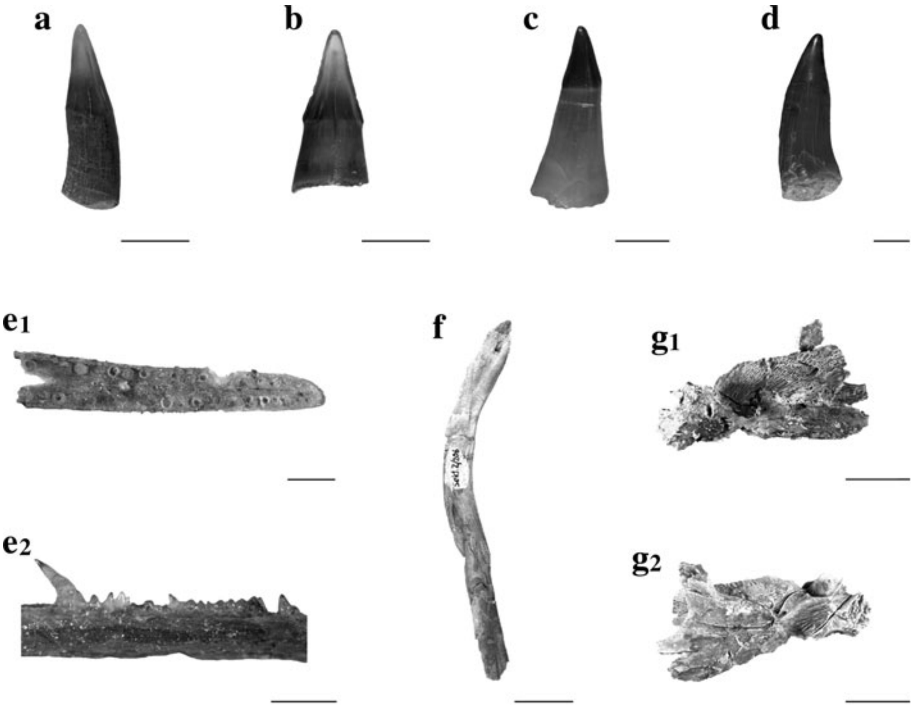

**Fig. 8** **a–d** Caturid and oligopleurid teeth. **a–b** *Caturus* sp. **a** NMS 20485, linguo-lateral view. **b** NMS 20510, lingual view. **c** NMS 20514, *Ionoscopus* sp., lateral view. **d** NMS 20513, *Callopterus* sp., lingual view. **e** NMS 20516, Aspidorhynchids, *Belonostomus* sp., lower jaw, in occlusal view (**e1**) and with detail of the right side (**e2**). **f** NMS 20518, Halecomorphi indet., right cleithrum of a large halecomorph fish. **g** NMS 20517, Osteichthyes indet., left lower jaw of a ?lobefin in labial (**g1**) and lingual (**g2**) view. *Scale bars* 2.0 cm (**f**), 1.0 cm (**g1**, **g2**), 0.2 cm (**e1**), 0.1 cm (**a–d**, **e2**)

*Ionoscopus* (NMS 20514, Fig. 8c) and one tooth may possibly be assigned to this species (NMS 20515, not figured).

*Callopterus sp. (NMS 20513)*

| | |
|---|---|
| Order | Ionoscopiformes Grande and Bemis 1998 |
| Genus | *Callopterus* Thiollière 1858 |

Teeth of *Callopterus* appear markedly larger and more fusiform than those of *Caturus* or *Ionoscopus* (Mudroch and Thies 1996). The stout tooth neck supports a comparatively blunt, curved enameloid cap with slightly arched and little prominent blades. Only one tooth could unequivocally be assigned to *Callopterus* sp. (NMS 20513, Fig. 8d).

Halecostomi

| | |
|---|---|
| Division | Halecostomi *sensu* Patterson 1973 |
| Subdivision | Teleostei *sensu* Patterson 1973 |
| Order | Aspidorhynchiformes Bleeker 1859 |
| Family | Aspidorhynchidae Nicholson and Lydekker 1889 |
| Genus | *Belonostomus* Agassiz 1834 |
| Type species | *Aspidorhynchus tenuirostris* Agassiz 1833 |

*Belonostomus sp. (NMS 20516)*

In the Solothurn assemblage, *Belonostomus* is represented by a near complete predentary (NMS 20516, Fig. 8e1). This comparatively well-preserved specimen is about 13.5 mm long and slightly damaged probably due to its delicate nature. In *Belonostomus* the enormously-elongated predentary is studded across its full length with large, conical teeth surrounded by simple, smaller teeth. On the premaxillary, however, the teeth are restricted to 2/3 of the posterior end and comprise large teeth only (Brito 1997). Large teeth are composed of a lingually-curved tooth-neck and a straight enameloid cap, both circular in transection (Mudroch and Thies 1996). In the Solothurn specimen, both types of teeth can be observed although some of the larger teeth are not present anymore (Fig. 8e2). The posterior end of the premaxillary seems to be damaged and the suture delineating the border to the prearticular is not recognizable. Thus, the total hypothetical length of the prearticular can only be estimated making an unambiguous identification difficult. A ratio of 7.5 between the prearticular length to height corresponds roughly with the ratio observed for the small Late Jurassic species *Beleonostomus tenuirostris* (6.0) and some large *Beleonostomus* species (10.0) from the Late Cretaceous (Brito 1997). Although difficult to accurately determine, the full size of the animal would merely have been between 15 and 20 cm, which is about half the size of an adult *Beleonostomus tenuirostris*. This could also explain the slight discrepancy in the prearticular ratio observed here and may be the result of ontogenetic variability between adults and juveniles rather than species divergence.

Osteichthyes indet. and Halceomorphi indet.
(*NMS 20517, NMS 20518, NMS 20520-20521*)

Two additional specimens of bony fishes could not be classified precisely, and are here mentioned only briefly. The first of the two specimens is represented by a right cleithrum of a large fish (NMS 20518, Fig. 8f). The bone is 13.5 cm long and probably belonged to a predatory fish, possibly *Caturus* (see also Lambers 1992, p. 130, fig. 18A). A rough estimation places the total length of the fish at approximately 1–1.5 m, a length also assumed for adult individuals of *Caturus* (Mudroch and Thies 1996). There are also a few diamond or paddle shaped scales of halecomorph predatory fish (NMS 20520 and NMS 20521, not figured) that were not identified any further but would possibly match a similar sized fish. The second specimen (NMS 20517, Fig. 8g1, g2) is harder to identify. A possible candidate for the spongious piece of bone could be a left lower jaw. In anteromedial view, the bone reveals the typical creases of the symphysis. A long process on the inside could be interpreted as a coronoid process. There is also an elongated edge along the dentary noticeable. Oral teeth were probably supported by prearticular or dermal bones. Particularly the large coronoid process of the approximately 3.5 cm long specimen suggests a member of the lobe finned-fish (Sarcopterygii). In this case, the total length of the fish probably did not exceed 40 cm.

## Concluding remarks

The Kimmeridgian Solothurn Turtle Limestone contains a rich community of fossil invertebrates and vertebrates. Vertebrates are represented by a wide spectrum of various fish types and marine reptiles, namely sea turtles and crocodiles, which inhabited a shallow lagoon (Meyer 1989, 1994b). This lagoon was protected in the southeast by sandbars but maintained a connection to open waters in the southwest (Meyer 1989; Meyer and Jordan 2000). The sandbars provided shelter against the open sea and represented an optimal nursery for a variety of juvenile fish species. This assumption is corroborated by both the findings of teeth from *Caturus*, a predatory fish that presumably fed on schools of small fish (Mudroch and Thies 1996) and an overwhelming number of rather small pycnodont jaws. However, it is important to emphasize that pycnodont odontogenesis and its implications on teeth preservation are still not fully understood (Kriwet 2004). Previous studies on coprolites have also shown that fish-hunting marine reptiles exploited the abundant food supply (Meyer 1989).

In Solothurn, pycnodonts are very common, possibly also embracing the highest diversity of species. They probably closely resembled extant coral fishes and were highly specialized and manoeuvrable (Mudroch and Thies 1996). Fast and agile predators, i.e. predatory fish and crocodiles most likely hunted both juvenile and adult individuals.

Amongst the predatory fish, *Caturus* is particularly well represented in Solothurn whereas teeth of its close relatives *Callopterus* and *Ionoscopus* were only found sporadically. These fish were powerful predators, equipped with light scales and symmetrical tail fins enabling high speeds when attacking prey. *Caturus* probably was a fast epipelagic predator whereas *Ionoscopus* and *Callopterus* most likely ambushed their prey by surprise attack (Mudroch and Thies 1996). *Belonostomus*, an elongated fish resembling the recent half-beak, probably used similar tactics (Mudroch and Thies 1996). The large number of benthic fish species relying on seabed cover such as *Ischyodus*, *Hybodus*, *Asteracanthus*, *Lepidotes* or ambush predators seeking cover behind floating seaweed or debris such as *Ionoscopus* and *Callopterus* suggest the former presence of bigger seaweeds, although there are no fossil remains of seaweeds known from Solothurn. *Belonostomus* and *Caturus* on the other hand may have merely visited the lagoon occasionally, whereas saltwater crocodiles (especially *Steneosaurus* and to a lesser degree *Machimosaurus*) seemed to have used the open connection from the sea into the lagoon more frequently (Meyer 1989).

**Acknowledgments** I thank C.A. Meyer (Naturhistorisches Museum Basel, Switzerland) for general support and insight into the historical, geological and palaeontological aspects of the excavation site. I would also like to thank the following people (in no particular order) for their valuable advice and discussion on identification of fish microvertebrates, fish systematics and paleoecology: D. Thies and A. Mudroch (Leibniz Universität Hannover, Deutschland), T. Bürgin (Naturmuseum St. Gallen, Switzerland), R. Kindlimann (Aathal, Switzerland), G. Viohl (Jura-Museum Eichstätt, Deutschland), H. Furrer (Paläontologisches Institut Zürich, Switzerland). Many thanks also go to W. Künzler (Curator Naturmuseum Solothurn, Switzerland), E. Müller and particularly to S. Thüring (Naturmuseum Solothurn, Switzerland) for technical support and the provision of crucial literature. Finally I would like to thank the editor D. Marty, and the two reviewers L. Cavin (Muséum d'Histoire Naturelle de Genève, Switzerland) and J. Kriwet (University of Vienna, Austria) for the great support I received when finalizing this paper.

## References

Agassiz, J. L. R. (1833–1844). *Recherches sur les poisons fossils*. Neuchâtel: Imprimerie de Petipierre (vol. 5).

Bräm, H. (1965). Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Paläontologische Abhandlungen, 83*.

Brito, P. M. (1997). Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnementales et biogéographiques. *Geodiversitas, 19*, 681–772.

Cappetta, H. (1987). *Handbook of paleoichtyology. In Chodrichthyes II, Mesozoic and Cenozoic Elasmobranchii (vol. 3B)*. Stuttart: Gustav Fischer Verlag.

Colombié, C. (2002). Sédimentologie, stratigraphie séquentielle et cyclostratigraphie du Kimméridgien du Jura suisse et du Bassin vocontien (France): relations plate-forme—bassin et facteurs déterminants. PhD thesis, University of Fribourg (Switzerland), GeoFocus 4.

Duffin, C. J. (2001). A chimaeroid (Holocephali, Chimaeriformes) vomerine toothplate from the Upper Cretaceous of Belgium. *Palaeontology, 44*, 1179–1188.

Duffin, C. J., & Thies, D. (1977). Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. *Geologica et Palaeontologica, 31*, 235–256.

Duncan, M. (2004). Chondrichthyan genus *Lissodus* from the Lower Carboniferous of Ireland. *Acta Palaeontologica Polonica, 49*, 417–428.

Egerton, P. G. (1847). On the nomenclature of the fossil chimaeroid fishes. *Quarterly Journal of the Gological Society, 3*, 350–353.

Jank, M., Meyer, C. A., & Wetzel, A. (2006a). Late Oxfordian to Late Kimmeridgian carbonate deposits of NW Switzerland (Swiss Jura): stratigraphical and palaeogeographical implications in the transition area between the Paris Basin and the Tethys. *Sedimentary Geology, 138*, 237–263.

Jank, M., Wetzel, A., & Meyer, C. A. (2006b). A calibrated composite section for the Late Jurassic Reuchenette Formation in northwestern Switzerland (?Oxfordian, Kimmeridgian *sensu gallico*, Ajoie-Region). *Eclogae Geologicae Helvetiae, 99*, 175–191.

Kriwet, J. (2004). Dental morphology of the pycnodontid fish †*Stemmatodus rhombus* (Agassiz 1844) (Neopterygii, †Pycnodontiformes) from the Early Cretacous, with comments on its systematic position. *Transactions of the Royal Society of Edinburgh, Earth Sciences, 94*, 145–155.

Kriwet, J., & Klug, S. (2004). Late Jurassic selachians (Chondichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity. *Zitteliana, A44*, 67–95.

Lambers, P. (1992). On the Ichthyofauna of the Solnhofen Lithographic Limestone (Upper Jurassic, Germany). PhD thesis, University of Groningen.

Lang, F., & Rütimeyer, L. (1867). Die fossilen Schildkröten von Solothurn. *Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesamten Naturwissenschaften, 22*, 1–47.

Longbottom, A. E. (1984). New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali. *Bulletin of the British Museum of Natural History (Geology), 38*, 1–26.

Meyer, C. A. (1988a). Subtidal lagoon communties of a Late Jurassic turtle-deposit from Northern Switzerland. Atti del Quarto Symposio di Ecologia e Paleoecologia delle Comunità Bentoniche (pp. 107–121). Torino: Museo Regionale di Scienze Naturali.

Meyer, C. A. (1988b). Ein neuer Seestern aus den Solothurner Schildkrötenkalken (Oberes Kimmeridgien: Kt. Solothurn). *Eclogae Geologicae Helvetiae, 81*, 843–856.

Meyer, C. A. (1989). Der Lebens- und Ablagerungsraum der Solothurner Schildkrötenkalke. *Naturforschende Gesellschaft Solothurn, 34*, 185–197.

Meyer, C. A. (1990). Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian, Lommiswil, Kt. Solothurn) of Northern Switzerland. *Eclogae Geologicae Helvetiae, 82*, 389–397.

Meyer, C. A. (1993). A sauropod dinosaur megatracksite from the Late Jurassic of Northern Switzerland. *Ichnos, 3*, 29–38.

Meyer, C. A. (1994a). *145 Millionen Jahre vor unserer Zeit*. Solothurn: Verlag Vogt-Schild AG.

Meyer, C. A. (1994b). Depositional environment and paleoecology of the Solothurn Turtle Limestone. *Geobios, 16*, 227–236.

Meyer, C. A., & Jordan, P. (2000). Stratigraphie, Paläontologie und Tektonik der Verena-Kette nördlich Solothurn (Exkusion A am 25. April 2000). *Jahersbericht und Mitteilungen des oberrheinischen geologischen Vereins, 82*, 17–28.

Mudroch, A., & Thies, D. (1996). Knochenfischzähne (Osteichthyes, Actinopterygii) aus dem Oberjura (Kimmeridgium) des Langenbergs bei Oker (Norddeutschalnd). *Geologica et Palaeontologica, 30*, 239–265.

Patterson, C. (1966). British Wealden Sharks. *Bulletin of the British Museum (Natural History), Geology, London, 11*(7), 284–350.

Peyer, B. (1946). Die schweizerischen Funde von *Asteracanthus* (*Strophodus*). *Schweizerische Paläontologische Abhandlungen, 64*, 1–101.

Peyer, B. (1954). Ein Gebissfund von *Lepidotus* aus dem oberen weissen Jura von Thayngen, Kt. Schaffhausen (Schweiz). *Schweizerische Paläontologische Abhandlungen, 70*, 1–20.

Poyato-Ariza, F. J. (2003). Dental characters and phylogeny of pycnodontiform fishes. *Journal of Vertebrate Paleontology, 23*, 937–940.

Poyato-Ariza, F. J., & Wenz, S. (2002). A new insight into pycnodontiform fishes. *Geodiversitas, 24*, 139–248.

Poyato-Ariza, F. J., & Wenz, S. (2005). *Akromystax tilmachiton* gen. et sp. nov., a new pycnodontid fish from the Lebanese Late Cretaceous of Haqel and En Nammoura. *Journal of Vertebrate Paleontology, 25*, 27–45.

Rees, J. (2008). Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology—preliminary results. *Acta Geologica Polonica, 58*, 217–221.

Rees, J., & Underwood, C. J. (2002). The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (Selachii). *Journal of Vertebrate Paleontology, 22*, 471–479.

Rees, J., & Underwood, C. J. (2008). Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). *Palaeontology, 51*, 117–147.

Rütimeyer, L. (1873). Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. *Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesamten Naturwissenschaften, 25*, 185.

Stahl, B. J., & Chatterjee, S. (1999). A late Cretaceous chimaerid (Chondrichthyes, Holocephali) from Seymour Island, Antarctica. *Palaeontology, 42*, 979–989.

Strasser, A. (2007). Astronomical time scale for the for the Middle Oxfordian to Late Kimmeridgian in the Swiss and French Jura Mountains. *Swiss Journal of Geosciences, 100*, 407–429.

Thalmann, H. (1966). Zur Stratigraphie des Oberen Malm im südlichen Berner und Solothurner Jura. *Mitteilungen der Naturforschenden Gesellschaft des Kanton Solothurn, 22*, 126.

Thurmond, J. T. (1974). Lower vertebrate faunas of the Trinity Division in North-Central Texas. *Geoscience Man, 8*, 103–129.

Underwood, C. J. (2002). Sharks, Rays and a Chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, Southern England. *Palaeontology, 45*, 297–325.

von Huene, F. (1926). Die Saurierfauna des Portlandkalkes von Solothurn. *Eclogae Geologicae Helvetiae, 19*, 584–603.

Waite, R. (2010). The palaeoecology of high-spired gastropods and the lost palaeosols: depositional reconstructions on a shallow carbonate platform (Late Kimmeridgian, Swiss Jura Mountains). PhD thesis, University of Fribourg (Switzerland), GeoFocus 23.

Woodward, A. S. (1895). Catalogue of fossil fishes in the British Museum (Natural History), 3, London.