

The Norian fish deposits of Wiestal („Seefeld Member“, Northern Calcareous Alps, Salzburg, Austria) – taxonomy and palaeoenvironmental implications

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KEYWORDS

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Abstract

The Alaunian Seefeld Member of the Upper Triassic, a dark grey laminated and bituminous dolomitic limestone succession outcropping near the Wiestal-reservoir lake northeast of Hallein (Salzburg, Austria) is known for its extremely rich ‘ganoid’ fish fauna since more than a century. A privately initiated excavation that took place from 2012 to 2014 yielded far more than a thousand well-preserved fish fossils recovered largely from five mm-thin fossil horizons. The actinopterygian assemblage is dominated by several growth stages of the highly variable ginglymodian *Paralepidotus ornatus*, allowing for a documentation of ontogenetic transformations in cranial and postcranial morphology, dentition and squamation patterns, associated with habitat and dietary shifts. Small-sized swarm-fishes such as the macrosemiid *Legnonotus* and the teleost *Pholidophorus* are rather common members of the assemblage, while the occurrence of the ginglymodian *Semiolepis*, the dapediid *Dandya*, the dwarfish pycnodont *Eomesodon* and the large predatory ‘palaeopterygian’ *Saurichthys* is restricted to rare individuals. A single scale of a large-sized coelacanth, a well-preserved, small lobster-like decapod, plant remains and coaly gagate derived from disarticulated driftwood belong to rare associated finds. Both the perfect preservation of all fossils and the bituminous laminated dolomitic limestones barren of microfossils argue for a deposition under anoxic conditions, most probably due to salinity stratification. The occurrence of complete swarms, partly showing isoorientation of fish carcasses in distinct layers, speaks in favour of recurrent and rapid mortality events triggered by upwelling anoxic bottom water, most likely released by severe tropical storms.

Zusammenfassung

Der obere Abschnitt des obertriassischen Hauptdolomits der Nördlichen Kalkalpen ist im Alaunium (Mittleres Norium, Ober-Trias) lokal als Intraplattformbecken-Spezialfazies mit bituminösen, feinst laminierten Dolomikriten ausgebildet. Aus dieser auch als „Seefelder Schichten“ oder „Seefeld-Subformation“ benannte Schichtenfolge wurde nordöstlich von Hallein (Salzburg, Österreich) nahe des Wiestal-Stausees bereits vor mehr als einhundert Jahren eine extrem individuenreiche, aber relativ artenarme Schmelzschupper-Fauna beschrieben. Eine von privater Hand organisierte und in den Jahren 2012 bis 2014 durchgeführte paläontologische Grabung erbrachte weit über eintausend gut bis sehr gut erhaltene Fischfossilien aus fünf unterschiedlichen, nur mm-mächtigen Fossil-Horizonten. Die Faunen-Assoziation besteht im Wesentlichen aus Actinopterygiern wird vor allem durch *Paralepidotus ornatus* in unterschiedlichen Wachstumsstadien dominiert. Die Funddichte dokumentiert ontogenetisch bedingte Variationen der cranialen und postcranialen Skelettmorphologie, des Zahnapparates sowie des Schuppenkleides, die alle an Änderungen von Lebensweise und bevorzugtem Habitat gekoppelt sind. Neben *Paralepidotus* treten relativ häufig kleinwüchsige Schwarmfische wie der Macrosemiide *Legnonotus* und der Teleostier *Pholidophorus* auf. Deutlich seltener ist der Ginglymode *Semiolepis*, der Dapediide *Dandya*, der Trennung! Pycnodontier *Eomesodon* sowie der große paläopterygische? Räuber *Saurichthys*. Weitere seltene Beifunde der Grabung waren eine isolierte Schuppe eines großwüchsigen Quastenflossers, ein kleiner, hummerähnlicher Krebs, diverse unbestimmbare Pflanzenhäcksel sowie zu Gagat umgewandeltes Treibholz. Die perfekte Erhaltung aller gefundenen Wirbeltier-Fossilien, der starke Bitumengehalt sowie die überlieferte Feinstlamination des sedimentären Gefüges sprechen für ein anoxisches, reduzierendes Ablagerungsmilieu, das vermutlich durch stratifiziertes, salzreiches Bodenwasser verursacht wurde. Komplett erhaltene, teilweise strömungsbedingt eingeregelter „Fischschwärme“ in unterschiedlichen, scharf voneinander abgegrenzten Horizonten deuten auf wiederkehrende lokale Fischsterben hin, vermutlich ausgelöst durch aufsteigendes, anoxisches, salzreiches Tiefenwasser während schwerer Tropenzyklone.

1. Introduction

Locally scattered across the Northern Calcareous Alps, the upper part of the Hauptdolomit-Formation (Northern Calcareous Alps, Upper Triassic) includes dark grey, bituminous and organic-rich, laminated dolomitic limestones (Figure 1). The organic content can reach up to 50% (Bechstädt et al., 1991; Lobitzer et al., 1994). Equal in lithological parameters but highly varying in local thickness, the succession was named after its type-locality in Seefeld (Tyrol, Austria) as “Seefeld Member” or “Seefelder Schichten” (Brandner and Poleschinski, 1986; Poleschinski, 1989; Hopf et al., 2001). It accumulated in tectonically induced, flat and small-scaled depressions which were located within an extended intertidal to subtidal carbonate platform area (reefal “Dachstein limestones” as well as lagoonal “Hauptdolomit” [Northern Alps] or “Dolomia Principale” [Southern Alps], see e.g. Czurda, 1973; Fruth and Scherreihs, 1982). The Dachstein limestone and, in particular, the Hauptdolomit are known to be poor or nearly barren of fossils (e.g. Kuhnert, 1967; Pflaumann and Stephan, 1968; Doben, 1973; Risch, 1993), which contradicts the general assumption of a highly diverse and complex subtropical ecosystem. Especially within the Hauptdolomit, evidence of ancient macrobiotic faunas as well as many of the microbiotic dwellers was obliterated by diagenesis – except the rare cases of very fine-grained, limy Seefeld successions with high organic content that underwent no further radical diagenetic and metasomatic processes. In general, the deposition of the organic-rich Seefeld Member points to anoxic conditions near the bottom and/or closely below the water-sediment boundary due to restricted water circulation and/or

evaporation-controlled water stratification (Bechtel et al., 2006). As for the Wiestal site, this is underlined by the virtual absence of any benthonic life as well as decomposing processes, and favoured the preservation of vertebrate remains (e.g. Tintori, 1992; Hopf et al., 2001; Wellnhofer, 2003; Saller et al., 2013) as remnants of the normally oxygenated and highly productive upper water column.

Within the Northern Calcareous Alps (NCA), the main distribution area of the Seefeld Member is situated between the Lechtal Alps in the west and the Wilde Kaiser-Mountains in the east – the sites represent small-scaled basins. Normally, the outcropped total thickness does not exceed a few metres with exception of the type locality. Hornung and Gruber (2011) described several m-thick occurrences of the Seefeld Member from the Karwendel Mountains near the German-Austrian borderline, only a few dozen kilometres away from the type locality, where the Seefeld Member amount to a total thickness of several hundreds of metres (Poleschinski, 1989).

From the area around Vorderriß (a village in the central Karwendel mountains), Frank (1993) and Kment (2004) specified a 50 m thick succession of “Ölschiefer” very similar to the Seefeld Member, however, barren of any fossils and stratigraphically belonging to the lower Hauptdolomit level.

Outside the central part of the NCA, occurrences of the Seefeld Member could be observed only in two regions: a) the Chiemgau Alps (Prien-Valley, see Ganss, 1980; Mühlau near Schleching, see Broili, 1914) and b) the Wiestal. The bituminous shales of Ölberg near Alland (Lower Austria, Austria) which have been recently assigned



Figure 1: Geographic map of the central and eastern parts of the Alps including the Northern Calcareous Alps (NCA). Highlighted outcrops of the fossil-bearing Seefeld Member as mentioned in the text: 1) Seefeld (type locality), 2) Karwendel Mountains (Vorderriß), 3) Schleching, Chiemgau Alps, 4) Wiestal and 5) Calcare di Zorzino, Lombardy, Italy.

to the Seefeld Member, however, are of Rhaetian age and thus part of the overlying Kössen Formation (Zapfe, 1950; Plöching, 1960).

Apart from its special lithological habitus, the Seefeld Member is famous for its well-preserved nektonic fauna, which is dominated by assemblages of ganoid fishes. Since more than one and a half century, macrofossils are known from several sites around Seefeld (Tyrol) (e.g. Kner, 1866, 1867; Deecke, 1898, 1927; Fischer, 1957; Bitterli, 1962), very sparsely from Schleching in the Chiemgau Alps (Bavaria) (see Broili, 1914), from the Wiestal (Gorjanović-Kramberger, 1905) and have been also discovered in the Southern Alps of Northern Italy ("Calcare di Zorzino", e.g. Tintori, 1992, 1996, 1998; Lombardo and Tintori, 2005).

The Seefeld Member of both the type-locality and the Wiestal site underwent intense mining: the rocks of the bituminous succession near Seefeld were distilled for the pharmaceutical oily compound called "Ichthyol". The mining in the Wiestal started already in times of the Roman Empire to obtain tesserae stones serving as a contrast to the Lower Jurassic red limestones of Adnet. Later on, the dolomitic limestones were mined for producing cement (Gorjanović-Kramberger, 1905). As in Seefeld, the industrial mining at the Wiestal site was finished in the 1960s. When the mining stopped, the frequency of fossil finds had decreased rapidly. Both facts led to cessation of the flow of scientific descriptions of the fish fauna for many decades and very little was known about it until the publication of Tintori (1996). As for the Wiestal area, no younger scientific publication has dealt with its palaeontological potential since Gorjanović-Kramberger (1905). In 1962, Griffith (1962) described the *Saurichthys* specimen of Schlosser (1918) which was allegedly found in "Adnet near Salzburg", but which comes most likely from the Seefeld Member of the Wiestal area, presumably from the "Hirtenstein quarry".

Since the second half of the 20th century, some excavation campaigns of private collectors took place at and around the "Hirtenstein Quarry". As no scientific benefit accrued from this digging campaigns and very little is known about the finds, this paper is thought as a summarising scientific "reprocessing" as well as a first inventory of our finds we collected through our excavation campaign from 2012 to 2014, now that most of our fossils are prepared or in the status of finishing preparation. Through the latter, some questions concerning the circumstances of embedding arose, including abiogenic features that caused mass mortality events and led to the enormous fossil enrichment in a few distinct horizons. The challenge would be to bring the new facts in line with already known and published sedimentary, geochemical and paleobiologic details.

2. The Wiestal site – a short historic review

The Wiestal site is located on the southern slope of the small forested Raucheck Mountain, overtopping the Wiestalstausee (Salzburg, Austria, see Fig. 2A-D). The

classic location is known as the "Hirtenstein Quarry". This outcrop, situated beside the old road from Ebenau to Oberalm, persisted through several centuries since the Roman mining, scientifically described first (and up to now exclusively) by Gorjanović-Kramberger (1905). He classified a collection of Hans Hoefer (former Professor at the University of Leoben, Styria) and erected several new ganoid fish taxa. However, as explained later in this paper, most of his postulated taxa do not withstand the present knowledge of evolution and biodiversity of Late Triassic actinopterygian fishes (Tab. 1). Interestingly, Gorjanović-Kramberger (1905) mentioned a small-sized "saurian" from the Hirtenstein Quarry, found by Dr. Franz Wähner (former Professor for Geology and Palaeontology in Zagreb, Croatia). However, no further specific details about this exceptional finding and/or the whereabouts of the fossil are known.

Within the time span between Gorjanović-Kramberger (1905) and the end of the 20th century, only two short popular science publications mentioned the Wiestal site regarding its fossil concentrations. Vogeltanz (1969) shortly described 'ganoid' fish fossils which were found incidentally during demolition of a baking oven on ground of the "Schönbauer" nearby the "Hirtenstein Quarry". Furthermore, the same author reported on the findings of H. Schaffer (a private collector from Upper Austria) from the "Hirtenstein Quarry" in a short newsletter-notice. There is only meagre information concerning this heavy-equipped excavation campaign and the whereabouts of the gathered fossils: aside from a plethora of 'ganoid' fishes, an unclassified turtle was found (G. Tichy, pers. commun.). Tichy (1987) mentioned the results of Gorjanović-Kramberger (1905) in the context of the history of palaeontological research of Salzburg. From 1970 to 1993, the "Hirtenstein Quarry" provided only rare findings, mostly single small- to medium-sized 'ganoid' fishes (detailed chronology in Moosleitner 2012a, 2012b; Moosleitner 2013 und Wolf et al., 2015).

The first excavation campaign outside the "Hirtenstein Quarry" was initiated by Gerhard Wolf (Bad Vigaun) in the year 1993. The excavation followed the hillside cut of the forest road to the Raucheck-Mountain and resulted in the discovery of a first specimen of *Saurichthys deperditus*. Currently, the 30 cm long specimen is exhibited in the palaeontological collection of the Burgmuseum Golling (Salzburg, see Wolf et al., 2015).

In 2008, a further excavation campaign was conducted by French and Austrian private fossil collectors on the ground "Stürkentoni" a few metres to the south from the 1993 site. Here, too, only few is known about the palaeontological benefit as no fossil found its way into a public collection and no (scientific) publication was carried out neither by the fossil diggers nor by local scientists, e.g. of the University of Salzburg.

3. Chronology of the recent excavation campaign

The recent excavation campaign started in summer 2012 on the ground of the "Schönbauer" site which is located

circa 50 m above the old road from Ebenau to Oberalm near Hallein. The official and exclusive permission of the landowner included that the limestone-succession was dismantled completely by hand and without the use of heavy equipment (e.g. pneumatic hammer).

In the first two years, the site was excavated in the north at an area of ca. 70 m² (Fig. 2E). By end of December 2013, the quarry face uphill had a maximum height of nearly 6 m. First results on the excavated actinopterygian fauna were published on an internet platform for palaeontology (Moosleitner, 2012a, 2012b, 2013). From January to end of March 2014, the excavation was continued southwards at an additional area of 15 m² (Fig. 2E). After ending of field work in April 2014, the lower fossil-bearing layers

were buried more than 1 m under excavation material. The plain was levelled as good as possible and the original working height of the uphill bank was thus reduced to ca. 3 m.

4. Material and Methods

4.1 Macrofossils

A small percentage of the gained fossils needed only minor or, in the best case, no further preparation, especially when the fossil-bearing beds have split amongst the fish-layers. If the beds are weathered, the colour of the matrix turns from dark- to bright-grey, showing a perfect contrast to the black or dark-brown ganoid scales.

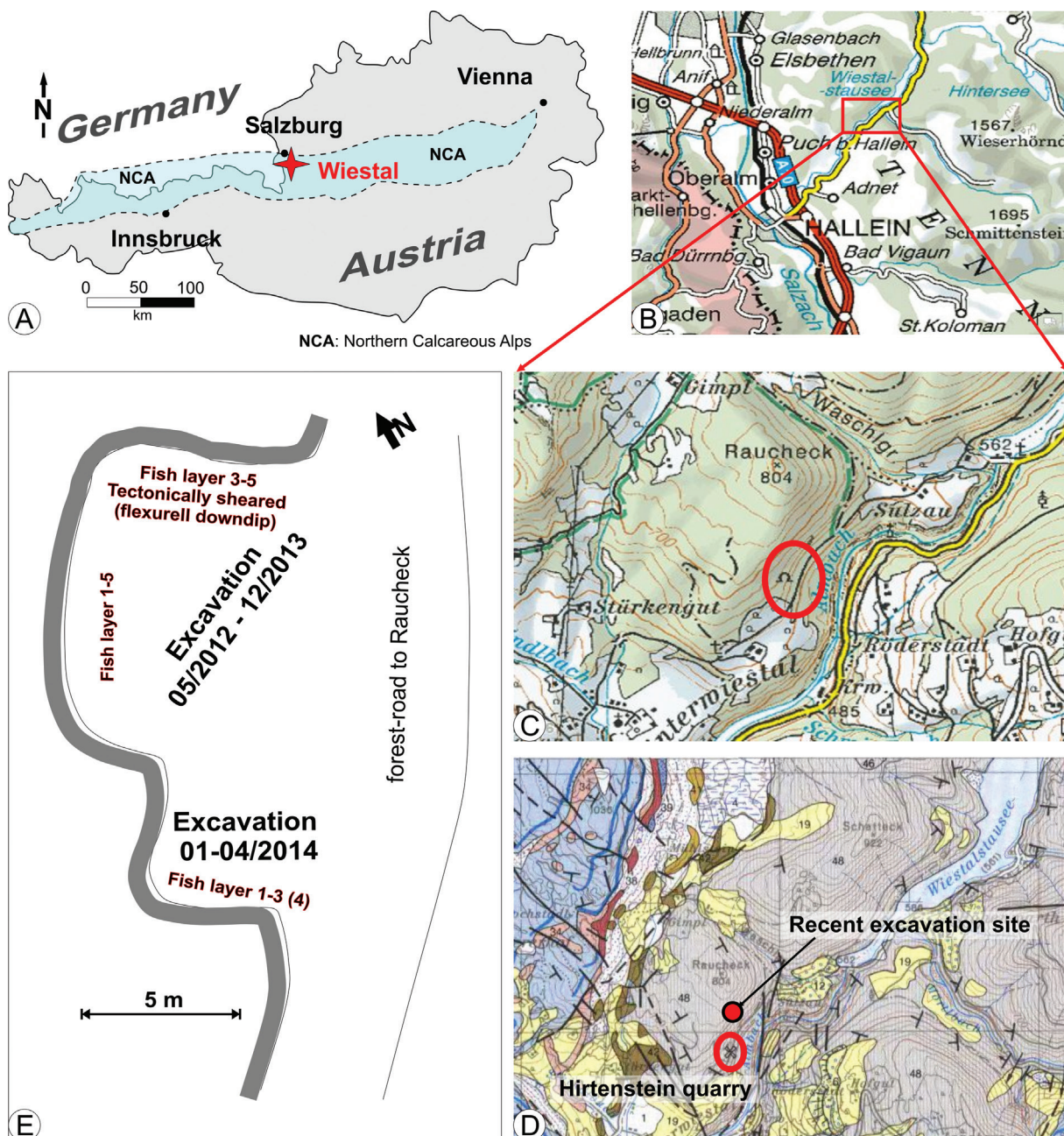


Figure 2: A & B: Geographic position of the Wiestal area (modified after AMAP-Austria, Vers. 2005). C: Geological map of the Wiestal area (courtesy of Geological Survey of Austria, Vienna). D: Sketch of the finding site on the southern slope of the Raucheck Mountain.

In this case, no further contouring of the fishes was necessary (Fig. 6). As unweathered and thus dark-grey coloured fossil-plates presented only an indistinct colour contrast difference between fossil and surrounding matrix, careful and fine contouring using a dental drill or fine graver was required, however, without to contact the fossil substance (Figs. 8-11). This method fails for preparing “swarms” of small-sized fishes providing a rather frail skeleton and tiny ganoid scales (Fig. 7). The emissive air of the pneumatic preparation tools would have swept them away.

Some large-sized specimens (Fig. 18D), which were collected in plate and counterplate, had to be prepared mechanically using a transfer-methodology as often done for fossils of the Upper Jurassic Lithographic Limestones of the Solnhofen region (e.g. Tischlinger and Völkl-Constantini, 2015 in Arratia et al., 2015). The vast majority of the collected plates and hand rock samples showed fossils in a cross-break. The fossil substance was visible only by its (sub)mm-thin blackish-brownish layer of broken scales. In this case, the fragments had to be glued carefully together with a two-part adhesive polyester resin, small pieces with fast-curing industrial superglue. Consequently, the fossil substance had to be exposed cautiously with an assortment of coarse to very fine hydraulic preparation tools (diverse gravers: HW-70/3; HW-90; HW-1; HW-325; Krantz-micrograver) adapted on a high-power compressor. Mechanic rasping by hand using an assortment of scalpels and needles failed due to the high durability of the Seefeld dolomitic limestones.

Most of the preparation was done by the authors (Hornung, van der Wielen). Some very rare material (e.g. *Saurichthys*, some large-sized *Paralepidotus*) was conveyed to the professional preparator Oliver Kunze (Stuttgart, Germany) or Michaela Wettlaufer (Mainz, Germany).

After finishing to uncover the fish fossils, the scratched surrounding matrix was planished either by a hydraulic graver with a chisel bit or by a DREMEL mortiser with adequate top parts.

The fish specimens of Wiestal presented here belong to the private collections of some of the above authors (abbreviations: collection Gerhard Wolf, Bad Vigaun: **CGW**; collection Joop van der Wielen, Salzburg: **CJW**; collection Thomas Hornung, Berchtesgaden: **CTH**; collection Burgmuseum Golling: **CBG**). The fossils are accessible under the above-mentioned addresses after prior appointment.

4.2 Microfossils

In order to achieve a high-resolution stratigraphic dataset of possible conodont assemblage-zones as done in Donofrio et al. (2003), the Wiestal site was sampled bed by bed. A dolomicrite sample of every excavated horizon (bed 1 to 18; weight max. 1.0 kg per layer) was dissolved in 10% formic acid and 90% deionized water for 48 hours. The diluted acid was changed every 18 hours after decreasing of the acid reaction in order to avoid acid crystallisation. The insoluble residue was washed and fractioned by sieving (very coarse: 500 µm; coarse: 250 µm; fine: 100 µm). To obtain retrievable results and avoid contaminations of subsequently washed material, repeated sieve-cleaning by ultrasonic baths was necessary. All material treated by micropalaeontological methods is stored at the Department of Geography and Geology, University of Salzburg (archive Hornung, “Wiestal”).

5. Litho- and Biostratigraphy

The Wiestal area, like many other regions within the Northern Calcareous Alps, is dominated by the Hauptdolomit, a thick succession of well-bedded, monotonous dolomitic mudstones, scarcely intercalated with few bioclastic wacke- and packstones as well as recrystallized algal laminated microbialites. Towards the top of the formation, more frequently beds occur containing intraformational breccias, conglomerates, resediments and microbialite horizons with shrinkage cracks, which indicate a shallow marine, tidal flat environment (e.g. Fruth and Scherreicks, 1973; Hopf et al., 2001).

Order	Family	Genus and Species (this paper)	Gorjanovic-Kramberger (1905)
Saurichthyiformes	Saurichthyidae	<i>Saurichthys deperditus</i>	-
Semionotiformes	Macrosemiidae	<i>Legnonotus krambergeri</i>	<i>Ophiopsis attenuata</i>
	Callipurbeckiidae	<i>Semiolepis bremanus</i>	<i>Semionotus kapfi</i>
		<i>Paralepidotus ornatus</i>	<i>Colobodus ornatus</i>
			<i>Colobodus elongatus/decoratus</i>
			<i>Heterolepidotus dorsalis</i>
Dapediiformes	Dapediidae	<i>Dandya ovalis</i>	<i>Spaniolepis ovalis</i>
Pycnodontiformes	incertus	<i>Eomesodon hoeferi</i>	<i>Mesodon hoeferi</i>
Pholidophoriformes	Pholidophoridae	<i>Pholidophorus latiusculus</i>	<i>Pholidophrus latiusculus</i>
			<i>Pholidophrus n.sp.</i>
			<i>Dapedius sp. aff. Costae</i>
			<i>Heterolepidotus parvulus</i>

Table 1: List of the ganoid fish fauna found at the Wiestal site during the actual excavation campaign and “translated” to the species which were erected by Gorjanović-Kramberger (1905).

The sedimentary transition between the middle and the upper Hauptdolomit in the Wiestal area contains an intercalation of the Seefeld Member which is exposed at the southern slope of the Raucheck-Mountain. This consists of a 10 m thick succession of very hard, thin- to medium-bedded, dark- to blackish-grey, bituminous dolomicritic limestones. Every bed is confined by a (sub-) mm-thick marly bedding plane. The individual beds show thicknesses between 10 and 60 cm, which can vary across short distances – some layers show a lateral dwindling within a few metres. Thus, the sedimentary succession as pictured in Figure 5 is idealized. Most of the horizons exhibit a very fine lamination at a sub-mm scale, often accompanied by synsedimentary load marks being similar to midget normal faults with mm-sized offsets (Fig. 3). The preservation of fine sedimentary lamination implies the absence of endobenthic sediment feeders such as small crustaceans, gastropods and annelids.

The stack of bituminous dolomicrites is assumed to be deposited coeval to a similar succession at the type-locality in Seefeld (Hopf et al., 2001; Donofrio et al., 2003). There, Donofrio et al. (2003) extracted some conodonts from tempestite layers and assigned the Seefeld Member into the time span between the base of the Alaunian 2 and the Sevatian 1 (Norian, Upper Triassic). However, the dolomicrites at the Wiestal site are devoid of microfossils (see also Bechtel et al., 2006).

At its type locality, the Seefeld Member can be subdivided into several regressional-transgressional cyclothems with a rather heterogeneous lithology, and encompass an overall thickness of nearly 500 m. The discrepancy in total thicknesses between the Wiestal area and the Seefeld type locality may be due to different basal subsidence rates on the one hand as well as different dimensions on the other hand. The upper part provides several fossil-rich “highly bituminous very fine laminites” with a thickness of several tens of metres (Donofrio et al. 2003) containing an actinopterygian fauna very similar to the one presented from the Wiestal site. The vertebrates are accompanied by plant fragments and rare flattened ammonoids. The enormous thickness of the Seefeld succession at its type locality suggests not coercively a deeper sedimentary intraplateau-basinal



Figure 3: Every single layer of the Seefeld Member at the Wiestal site (thickness approximately 5 cm) shows a fine lamination, partly with synsedimentary („listric“) load casts.

environment but rather an increased local subsidence induced by enhanced tectonic activity as compared to the Wiestal site.

Detailed geological mapping of the southern slope of the Raucheck-Mountain between the “Hirtenstein Quarry” and the excavation site above (Hornung, pers. obs.) has shown that the sedimentary succession of the upper Hauptdolomit including the Seefeld Member dips gently towards SW and is displaced by listric, NW-SE striking normal faults. Thus it seems that the laminated dolostone succession is occurring at different lithostratigraphical levels, which are, however, part of a single flat depression within the Hauptdolomit lagoon with dimensions of somewhat 300 m from the one end to the other.

6. Succession of the fossil-bearing layers at the Wiestal site – a short summary

Previous authors (Gorjanović-Kramberger, 1905; Griffith, 1962; Vogeltanz, 1969) describing fossils from the Wiestal site, have not collected the specimens by themselves and did not consider the lithology, sedimentology, lithofacies, palaeoecology and taphonomy of the site. Is there only one fossil-bearing horizon? Are there many? Are all fossils as perfectly preserved as shown in Gorjanović-Kramberger (1905) or do disarticulated carcasses also occur? Are the fishes preserved isolated or are there complete “fossil swarms”? Are the fishes arranged randomly or do they show isoorientation? As we knew from hearsay before our excavation campaign, all ‘ganoid’ fish fossil findings in the Wiestal region were believed to originate from one single, only mm-thick horizon in the lower part of the outcropping succession of the Seefeld Member, showing a fossilized pile preservation of the carcasses without intermediate sediment. Since this layer was known amongst fossil hunters since decades, we named it the “main layer” (Fig. 4A-C).

However, during the excavation in 2013, four new fossil layers beneath the “main layer” came to light that yielded horizon-specific actinopterygian fish assemblages in consistently good preservation, partly isolated, partly gathered in swarms, partly arranged randomly, partly preserved with consistently isooriented bodies (Figs. 8, 9 & 11).

Exceptionally, a few small- to medium-sized actinopterygian fishes were found completely isolated in the lower part of the succession (bed 2 & 3). Only the “main layer” showed consistently a fossilized pile of fish carcasses, the subjacent fossil horizons yielded complete fish swarms with tens or hundreds of fish bodies lying next to each other.

The following subchapters summarize the observations made in every single fossil-bearing layer, noted from the top-level down to the bottom of the excavated site.

6.1 Fish-layer 1 (bed 9) – „main layer“

Approximately 13 cm above its base, the 40 cm thick bed 9 contains the “main layer”: within 5 mm thickness, a plethora of actinopterygian skeletons are randomly

arranged in a fossilized pile (Fig. 4). As the horizon consists completely of mealy and crumbly fossil substance, it forms a predetermined breaking plane. This is a crucial disadvantage as several cleavage planes run through the fossil layer and the fishes, often rupturing them apart into plate and counterplate. Complex preparation is necessary in order to receive suitable and classifiable specimens that are concealed in the stack of partly preserved, torn specimens. Thus, preparation of complete fishes is

rather time-consuming. As it is demonstrated in Figure 6, the fossil assemblage is dominated by all growth stages of the morphologically variable species *Paralepidotus ornatus* (Agassiz), besides rare, small-sized *Pholidophorus*.

The “main layer” was a constant marker horizon at the main excavation site – on the location that was dismantled in the timespan from early winter 2013 to early spring of 2014 (Fig. 2E); however, the layer is thinning out completely towards the south (Fig. 5).

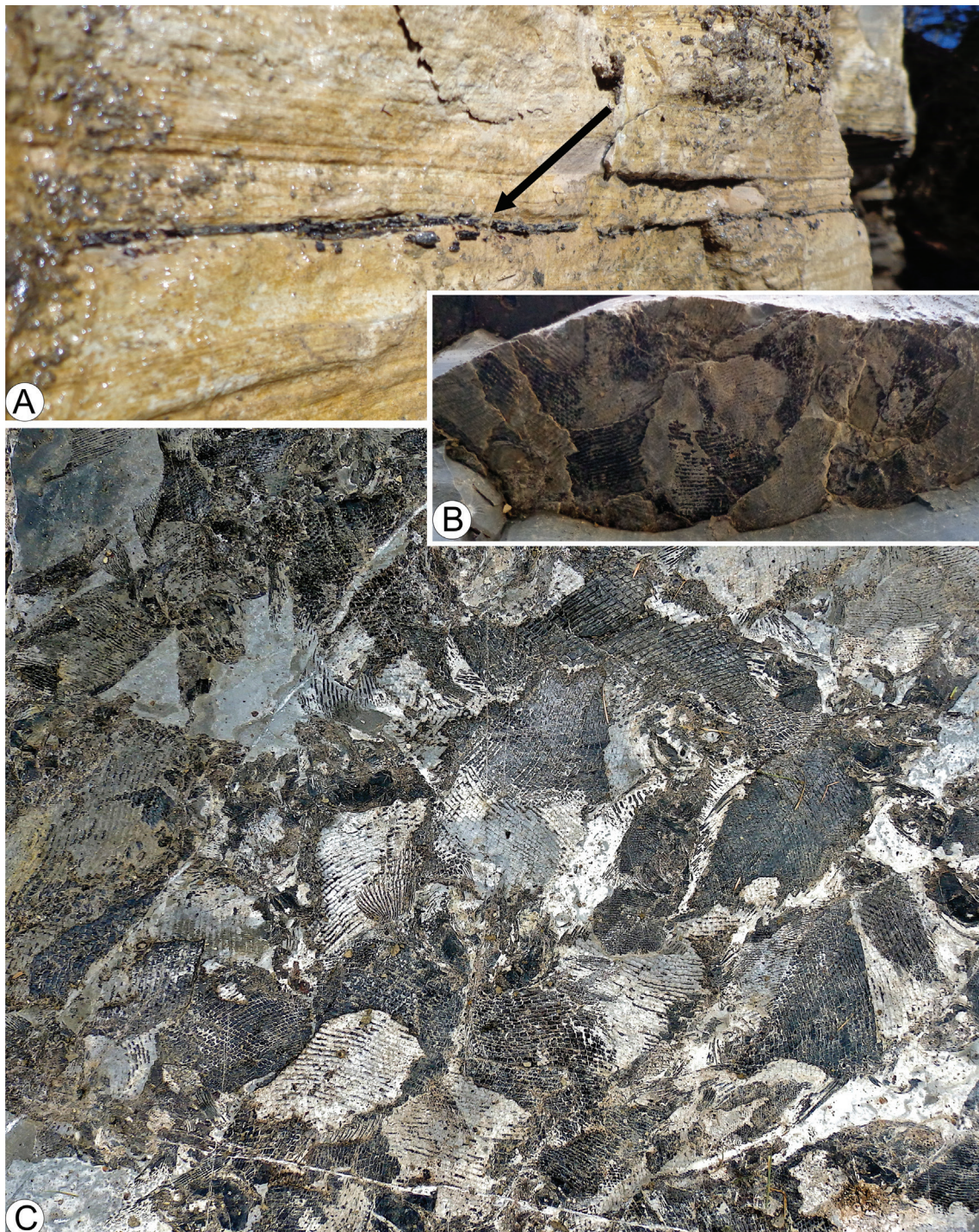


Figure 4: Picture A: Within the outcrop, the fish-layer 1 can be easily noticed by a ca. 5 mm thick tie, which completely consists of brownish to blackish coloured ganoid scales. Picture B shows the layer in the uphill quarry face, picture C a detail from a large, yet unprepared plate with numerous randomly arranged fish bodies (CGW).

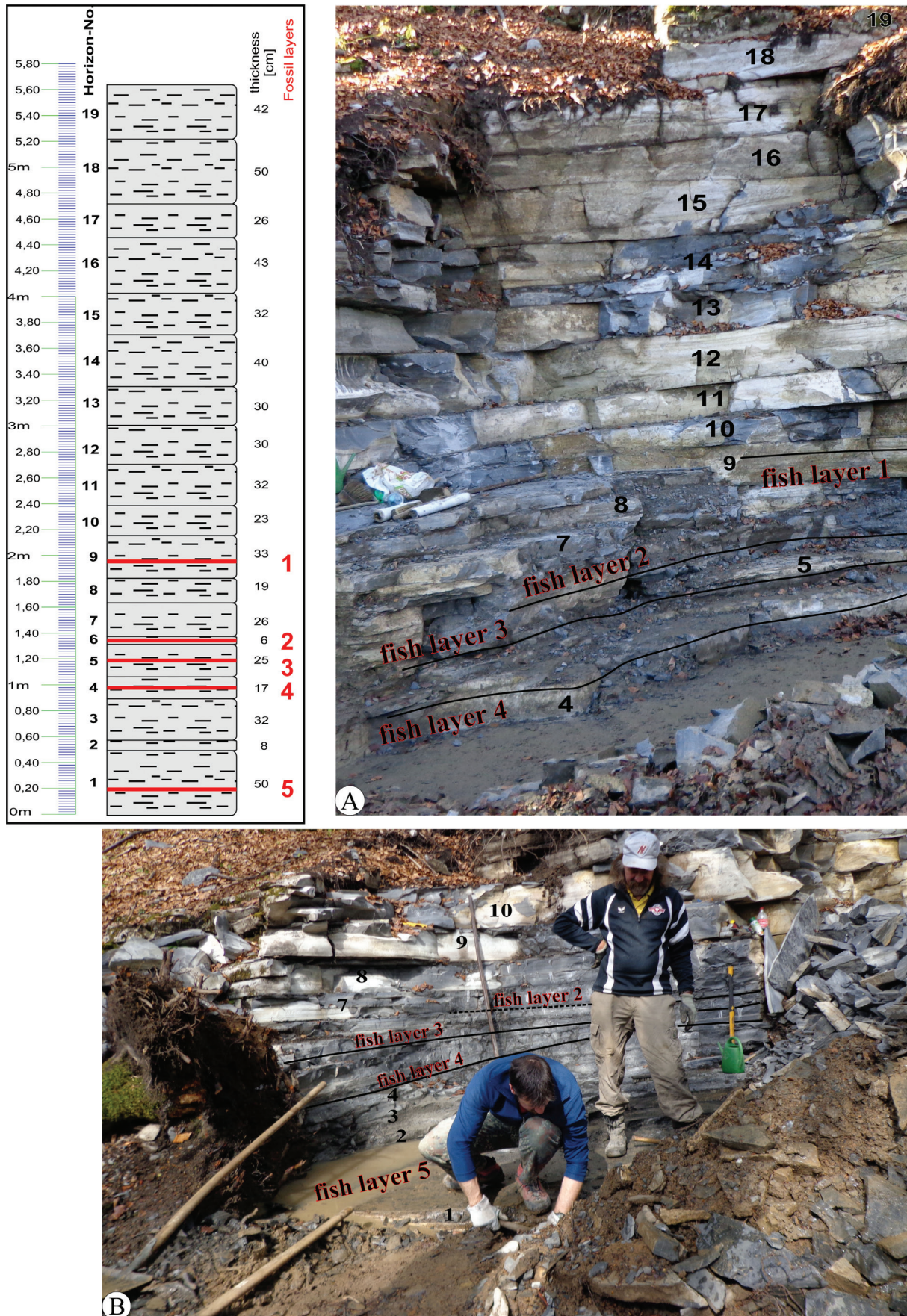


Figure 5: Composite log of the succession of the excavated Seefeld Member at the Wiestal site. Note the distinct fossil-bearing horizons in the lower part of transect. Picture A shows the excavation site that was exposed until December 2013, picture B the 2014 excavation site with the the lowermost excavated fossil horizon in early spring 2014 ("black layer", bed 1"): here it was obvious that the "Main Layer" (bed 9) dwindled towards S of the excavation site.

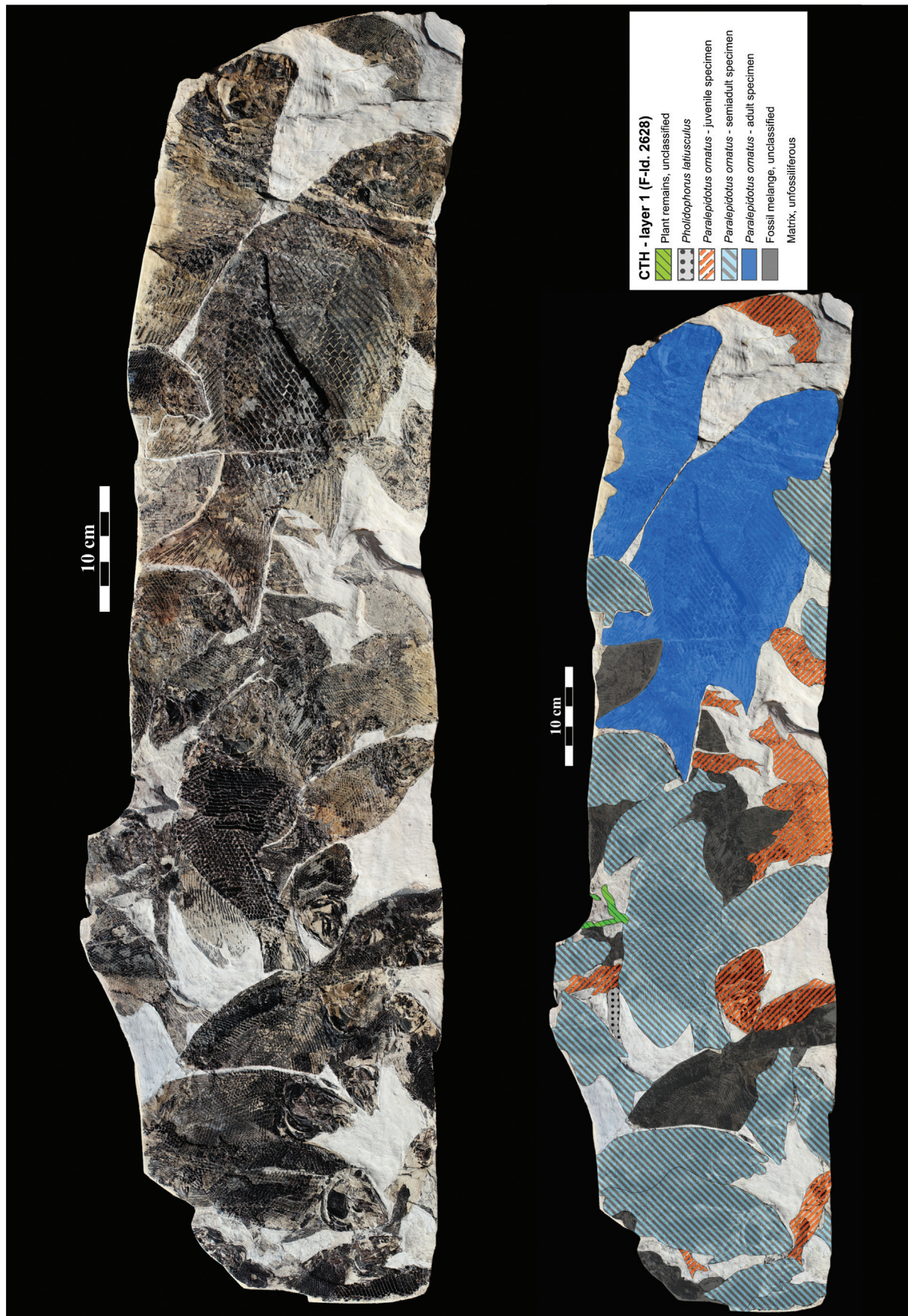


Figure 6: Example of a prepared large fossil-plate from bed 9 (fish layer 1: “main layer”) showing nearly exclusively juvenile to adult growth stages of *Paralepidotus ornatus* with rare *Pholidophorus latiusculus* and indeterminable plant fragments (CTH). Note the randomly arranged orientation of the fish carcasses. Abbr.: F-Id => “Fossil-ID, collection Hornung)

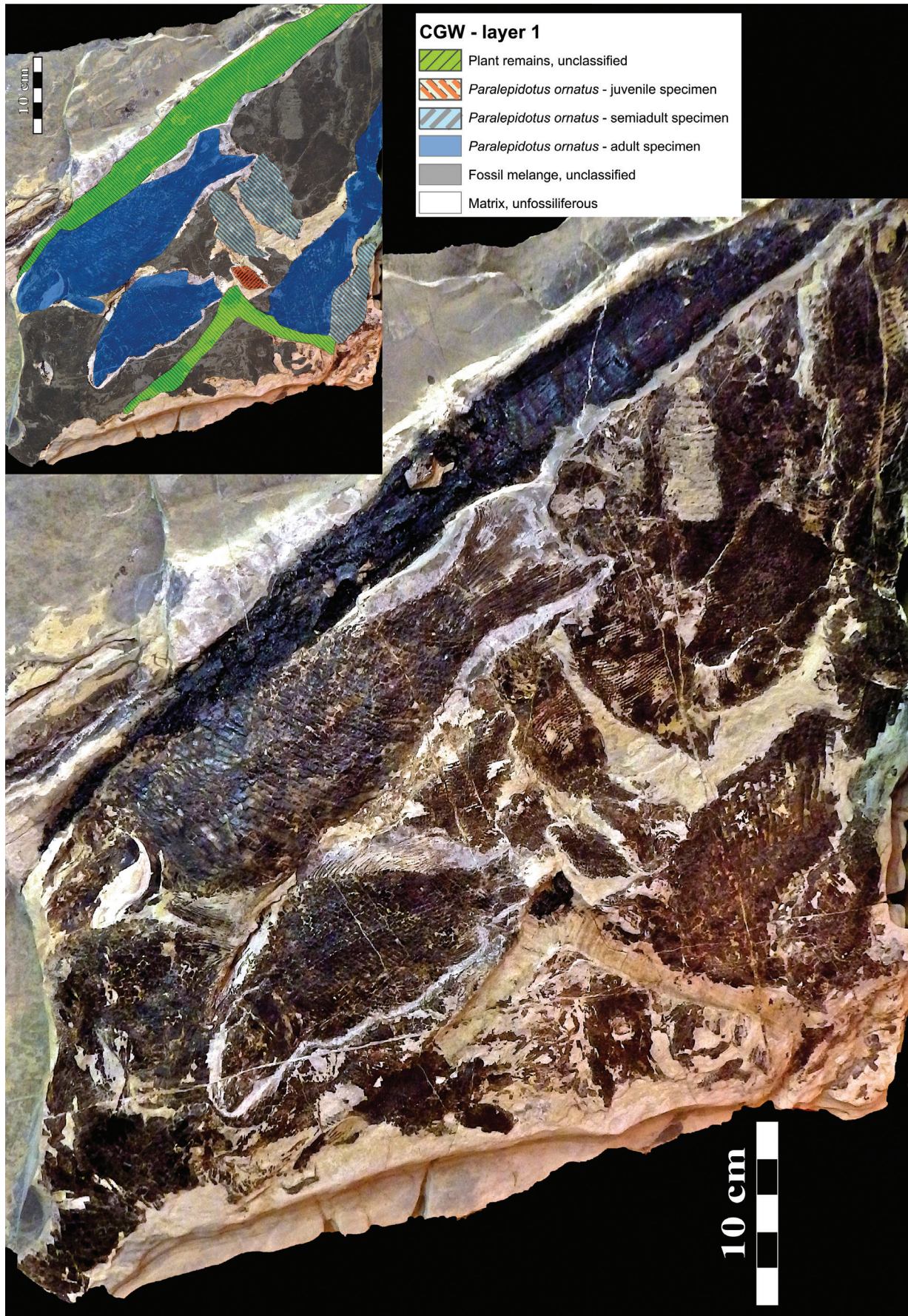


Figure 7: Example of a prepared large fossil-plate from bed 9 (fish layer 1: “main layer”) showing nearly exclusively juvenile to adult growth stages of *Paralepidotus ornatus* with rare *Pholidophorus latiusculus* and large gagate plant fragments (CGW).

6.2 Fish-layer 2 (bed 6)

Bed 6 has an overall thickness of only 6 cm. Approximately 5 mm beneath its upper bedding plane, a wafer-thin layer contains a fish fauna that is dominated by far by small-sized *Legnonotus* and *Pholidophorus* (size 3-6 cm), minor juvenile *Paralepidotus ornatus* as well as –

with extremely rare occurrence – the dapediiform *Dandya ovalis* (Figs. 8, 21B) as well as rare specimens of the small-sized pycnodont *Eomesodon hoeferi* (Figs. 22, 23). Similar to fish-layer 1, all fishes are arranged randomly but show no stacked embedding. Some specimens of *Pholidophorus* exhibit the characteristically arched vertebral

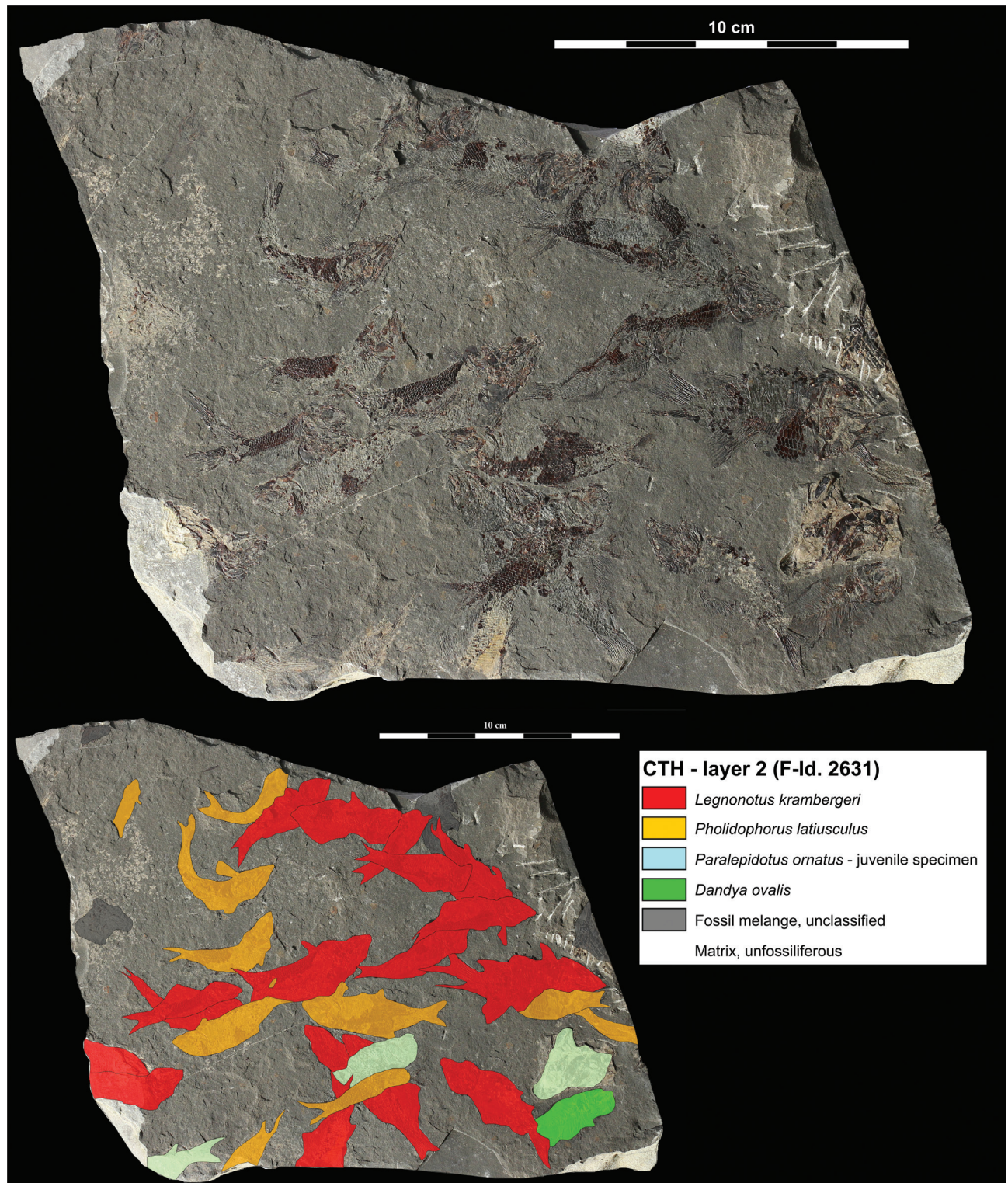


Figure 8: Medium-sized plate from bed 6 ("fish layer 2") showing a random arrangement of a fish-swarm dominated by *Legnonotus krambergeri* and *Pholidophorus latiusculus*. Remnants of *Paralepidotus ornatus* are only accessory – note the very rare dapediid *Dandya ovalis* in the bottom right corner (CTH).

column that was deformed through contraction of the vertebral musculature during necrotic processes (Viohl 1994).

The connection between fossil substance and matrix is often very disjointed. Thus, the preparation of the *Legnonotus-Pholidophorus*-swarms is precarious, as scattered fragments of the ganoid scales were too small and fractural to be put back in the original position.

6.3 Fish-layer 3 (bed 5)

Bed 5 has an average thickness of 25 cm and contains “fish layer 3” approximately 10 cm above its base. Most of the collected fish carcasses are more or less bedded within this distinct zone of 2-3 mm thickness. However, single specimens can also appear rarely at different levels within the complete layer – even lying on the upper bedding plane within the confining thin marly layer to the overlying bed 6. The fish fauna is dominated – again – by different growth stages of *Paralepidotus ornatus*, common *Pholidophorus latiusculus* and rare *Legnonotus krambergeri* as well as plant remains. The species *Semiolepis bremanus* was found only once in this horizon (Fig. 9). As most of the small- to medium-sized fishes show isoorientation and the lithology allows the recovery of large-sized plates, fish layer 3 provided fossil arrangements of a high aesthetic quality (Fig. 9).

During the excavation from 2013 to 2014, this layer featured some extraordinary well-preserved, large-sized specimens of *Paralepidotus*. The largest specimen has a standard length of 87 cm (Fig. 18D). This size is far beyond the one postulated by Tintori (1996; maximum size ~ 50 cm) for this genus.

The characteristic clustering of large-sized *Paralepidotus* in this distinct layer suggests the occurrence of swarms of adult specimens: Figure 10 shows a 60-cm-sized plate with two large *Paralepidotus* which crosswise overlap in the postcranial part (CGW).

The largest yet recovered, coherent assemblage of adult *Paralepidotus ornatus* is a 1 m-sized plate that contains three specimens: the largest specimen has an overall length of 57 cm, the smaller two fishes (50 and 42 cm) overlap crosswise (CTH). Whereas the largest fish is preserved in lateral view, the skull of the second-largest has been conserved slightly oblique showing the complete frontal.

Aside from the large-sized *Paralepidotus ornatus*, the fossil layer yielded rare *Legnonotus* and *Pholidophorus*.

6.4 Fish-layer 4 (bed 4)

Bed 4 shows an average thickness of 17 cm and contains the fourth fish layer. Similarly to the overlying bed 5 (“fish layer 3”), the fish fauna is dominated by juvenile and subadult growth stages of *Paralepidotus ornatus*, accompanied by common *Pholidophorus latiusculus* and *Legnonotus krambergeri*. Large-sized specimens, such as adult *Paralepidotus ornatus*, are absent. The special feature of this fossil assemblage is the strict orientation of nearly all fish carcasses. The direction of orientation,

however, seems to depend on the fish body size. Figure 11 shows an 80 x 60 cm-sized plate with nearly 100 isooriented juvenile *Paralepidotus*, *Pholidophorus* and *Legnonotus* as well as four subadult *Paralepidotus*, which, however, are directed at an angle of 30° clockwise to the swarm of small-sized ganoid fishes (CTH). This obviously size-dependent direction of orientation is not consistent through all finds obtained from this layer – Figure 12 shows uniform orientation of all fishes, regardless of their size (CGW).

6.5 Fish-layer 5 (bed 1 – “black layer”)

During our excavation campaign, bed 1 was used as the reference level. Owing to a mm-thin, deep black marly gouge on its very base, we called this horizon the “black layer”. Bed 1 possesses an average thickness of 50 cm and turned out to be the layer of the highest hardness we have dismantled. Approximately 30 cm underneath the top, it revealed the lowermost fish-bearing horizon (“fish layer 5”). The fossil assemblage consists mainly of different growth-stages of *Paralepidotus* as well as the small genera *Pholidophorus* and *Legnonotus*. Contrary to the two overlying fossil horizons, all fish bodies are embedded randomly, oftentimes packed as closely as in the “main layer” in bed 9 (Fig. 13).

During excavation in summer 2013, an extremely rare *Saurichthys deperditus* in an extraordinarily good preservation was found. The specimen pictured in Figures 13 and 14 (CGW) exhibits soft part preservation and a probable stomach content.

7. Taxonomy – systematic palaeontology

The following chapter is intended to summarize and describe all fossil groups we found during our excavation campaign. Note that the observations on the following fish species are described rather condensed. For more detailed explanations please consult the given citations.

Class **Osteichthyes** Huxley, 1880

Subclass **Actinopterygii** Cope, 1887 (sensu Rosen et al., 1981)

Infraclass **Chondrostei** Müller 1845; (**Palaeopterygii** Regan, 1923)

Order **Saurichthyiformes** Aldinger, 1937

Family **Saurichthyidae** Owen, 1860 [sensu Stensiö, 1925]

Genus **Saurichthys** Agassiz, 1834

Saurichthys deperditus (Costa, 1862)

Figures 13, 14, 15

1856 *Palaeoniscus* – Costa: 40-41. Pl. IV Figure 5.

1862 *Giffonus deperditus* – Costa: 26, Pl. VI Figure 2.

1862 *Acipenser?* – Costa: 33, Pl. V Figure 6.

1892 *Belonorhynchus* sp. – Bassani: 5ff.

1896 *Belonorhynchus* sp. – Bassani: 184, Pl. X, Pl. XV Figure 48, 49.

1918 *Saurichthys Krambergeri* – Schlosser: 94, Figure 158.

1923 *Saurichthys Krambergeri* – Schlosser: 96, Figure 158.

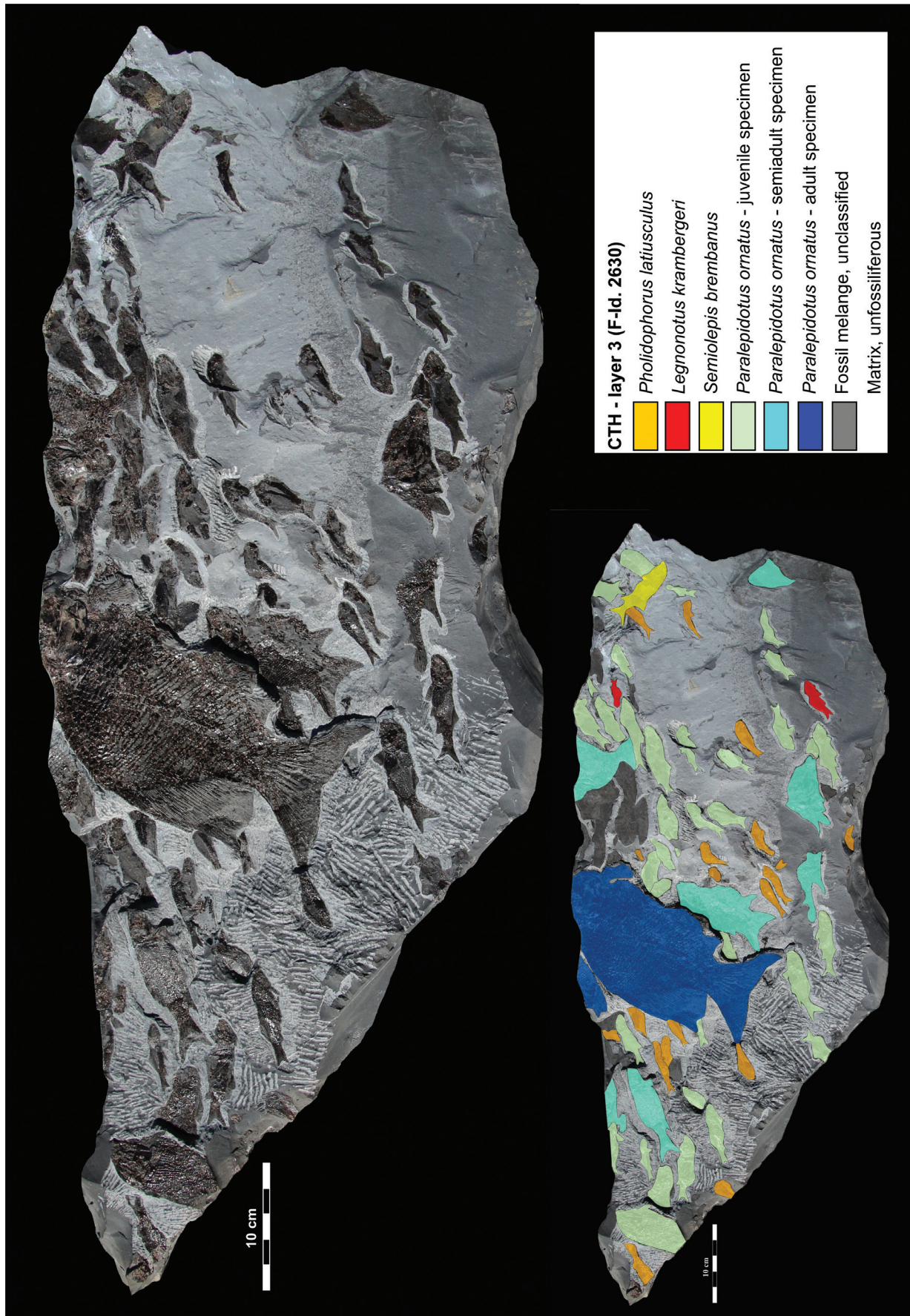


Figure 9: Large-sized plate from bed 5 ("fish layer 3") showing the isoorientation of small- to medium-sized fish carcasses, dominated by juvenile and subadult growth stage of *Paralepidotus ornatus* and completed by common *Pholidophorus latiusculus* and rare *Legnonotus krambergeri*. Note the rare semiontid *Semiolepis brembanus* (?juvenile growth stage) in the left upper corner (CTH).

1962 *Saurichthys krambergeri* – Griffith: 344, Figures 1–3, Pl. 50.

2005 *Saurichthys deperditus* – Tintori and Gozzi: 251.

2013 *Saurichthys krambergeri* – Schultz and Piller: 135, Pl. 16 Figure 3.

Locus typicus: Monte Pettine, Giffoni Vallepiiana (Salerno, Italy)

Stratum typicum: Upper Triassic: “Dolomia Principale” (Norian) sensu Tintori et al. (1985).

Holotype: Palaeontological Museum, Naples University, Italy: M126 – Costa (1862): plate 6, figure 2 (fragment of the caudal body part and fin).

Remarks: In the 3rd edition of Zittel’s Textbook of Palaeontology (Zittel 1920), the taxon *Saurichthys* has been illustrated by a complete specimen from the Upper Triassic of “Adnet” near Salzburg, with the name *Saurichthys krambergeri* Schlosser (1918), given in the figure caption. The first and only morphological description of the single specimen was published by Griffith (1962). Re-investigation of this fossil and further material, carried out in Gozzi’s (2006) unpublished thesis, led Tintori and Gozzi (2005) to the conclusion that *S. krambergeri* is morphologically indistinguishable from *S. deperditus* (Costa, 1862), and should therefore be regarded as a junior synonym of the latter. It should be noted that Gozzi (2006) pointed out several inaccuracies in the original description of *S. deperditus* by Costa (1856, 1862) and Bassani (1892, 1896).

Material: One nearly complete adult specimen without the caudal fin (found in autumn 2012) is preserved on plate and counterplate, partly with soft part preservation (Fig. 14). Two subadult specimens are preserved on plate

and counterplate (Figs. 15A, B): one specimen is preserved complete; the other is, again, preserved without the caudal fin. One fragment of the proximal torso without paired fins was found within excavation material. The first three specimens are stored in CGW, the latter fragmented specimen is currently at the Institute of Geology and Palaeontology in Freiberg / Germany to be prepared by IK. A further subadult specimen, used mainly for the description of caudal morphology (363 mm total length), is on display in CBG.

Description: *Saurichthys deperditus* is a very large actinopterygian (total length up to 164 cm: Gozzi, 2006; up to 113 cm in Austrian specimens), with the following saurichthyid-typical characteristics (see Romano et al., 2012; Tintori, 2013; Kogan and Romano, 2016): body elongate and slender, head elongate (about ¼ of total length) tapering anteriorly. The marginal dentition consists of large conical teeth with a vertically striated base and a rather smooth apical cap, alternating with smaller teeth of the same morphology. The axial skeleton is represented by a persistent notochord (not fossilized) with a bilaterally symmetrical series of dorsal arcual elements (neural arches) and perhaps corresponding ventral ossifications in the caudal body part, extending horizontally to the posterior end of the tail fin. The squamation is reduced to longitudinal rows of ossified scales in mid-dorsal and mid-ventral position and possibly a discontinuous series of small circular ossifications along the lateral line. The pelvic, dorsal and anal fins are situated in the posterior half of the trunk. The dorsal and anal fins are opposed and of similar size and shape to both lobes of the caudal fin.

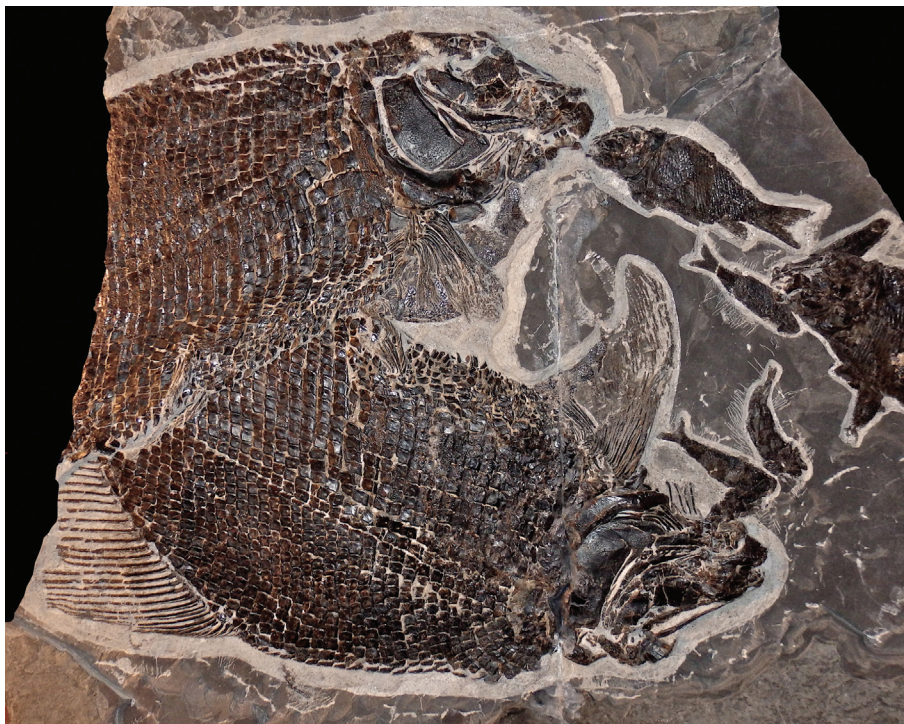


Figure 10: Large-sized plate (diameter ca. 60 cm) with different growth stages of *Paralepidotus ornatus* from bed 5 (“fish layer 3”, CGW).

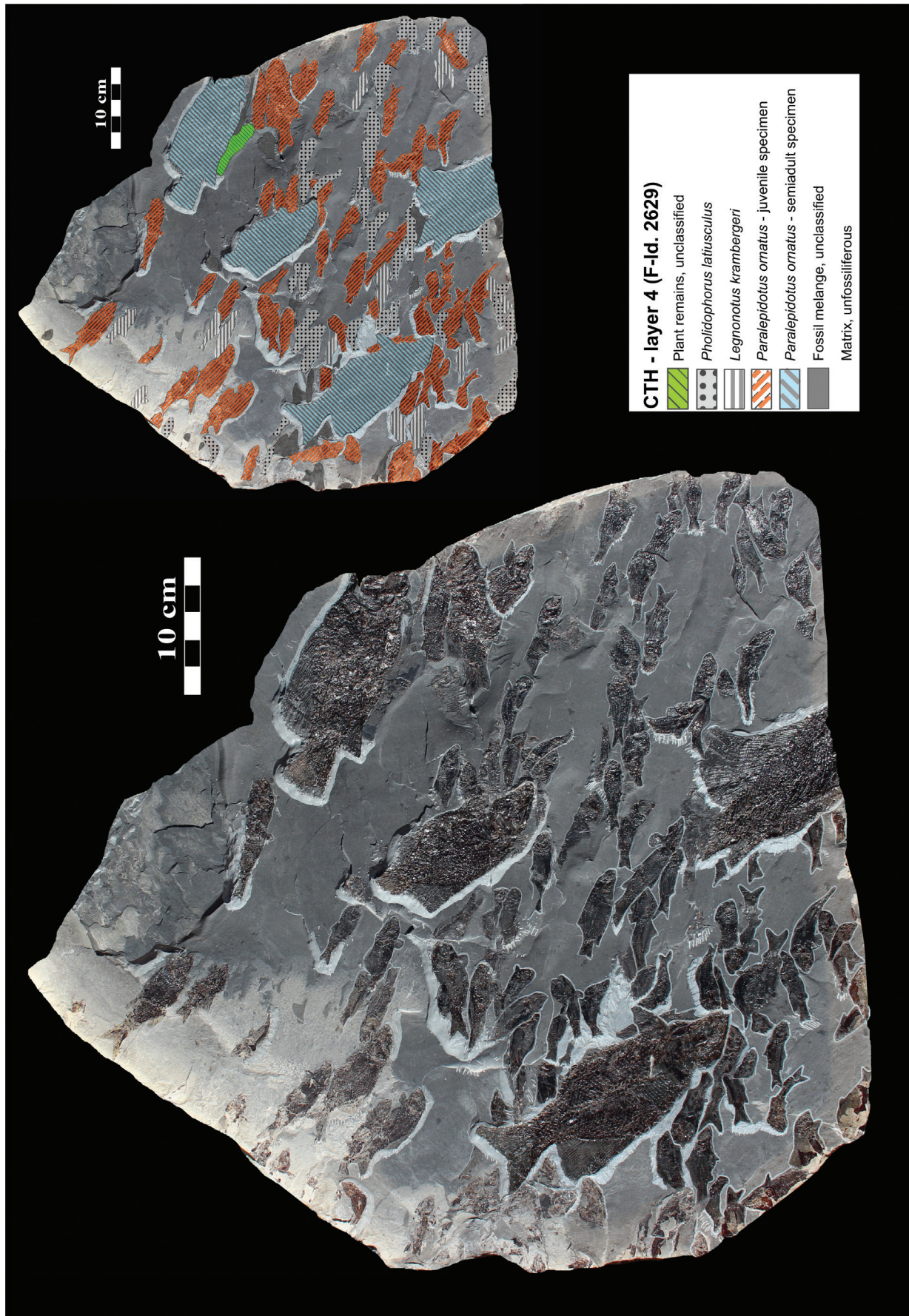


Figure 11: Large-sized plate (80 × 60 cm, CTH) showing a swarm of numerous, strictly orientated juvenile growth-stages of *Paralepidotus* as well as *Legnonotus* and *Pholidophorus*. Note the four medium-sized subadult growth stages of *Paralepidotus* that show a different mode of isoorientation, which is directed in an angle of ca. 30° with respect to the smaller fish bodies.

Saurichthys deperditus exhibits several morphological traits whose unique combination defines the species. In the anterior part of both the upper and the lower jaw, where the larger teeth are concentrated, occlusion is facilitated by the presence of “incisivlücken” accommodating larger teeth from the opposing jaw. The teeth themselves cluster within three size classes (about 5 mm, 2 mm and < 1 mm in height, respectively) and possess an unusually high apical cap showing faint vertical striae. The opercle is subrectangular and 1.5–2 times higher than long (18 mm to 9 mm in the subadult CBG specimen, 31 mm to 20 mm in the largest CGW specimen).

The dorsal arcual elements of the axial skeleton, placed symmetrically on both sides of the notochord, possess long projections directed anterodorsally (praezygapophyses) and posterodorsally (neural spines), the latter of which are laterally compressed and set closely to each other, forming a nearly continuous keel. Both projections point nearly vertically in the anteriormost abdominal body part. The praezygapophyses lie medially to the neural spines, which makes it difficult to observe their exact shape and size; in the mid-body region, it is clear that one praezygapophysis spans at least four arcual elements anterior to the one it belongs to (Fig. 15G), a pattern called ‘grid structure’ by Tintori (2013). In the anterior body portion, every second neural arch is pierced by a foramen (Fig. 15D). Ossified ventral arcual elements are restricted to the posteriormost part of the vertebral column behind the dorsal and anal fins (Fig. 15D). The mid-dorsal scale row starts just posterior to the head and consists

of narrow, lanceolate scales increasing in size posteriorly until the midpoint of the caudal peduncle, with the last ca. eight scales modified into broad scutes. The mid-ventral scale row begins farther posteriorly along the trunk (between the skull and the pelvic fins) but corresponds morphologically to the mid-dorsal one. Immediately behind the insertion of the pelvic fins, the ventral scale row bifurcates to form the anal loop, consisting of at least five elements on each side. In the caudal body part, some small circular ossifications occur that may be interpreted as the lateral line scales. The lateral line sensory canal can be traced as a discontinuous line paralleling the vertebral column in the abdominal body part of the upper specimen of Figure 15A, indicating that the canal had not necessarily to be embedded in scales. Morphology of the paired fins is difficult to assess due to imperfect preservation, but each of them (both pectoral and pelvic) seems to consist of about 30 unsegmented lepidotrichia, the longer of which bifurcate distally. The dorsal fin comprises about 38 lepidotrichia, the longest of which consisting of at least eight segments; in the anal fin, 34–42 fin rays can be counted, the longest being subdivided into at least six segments. Each lobe of the caudal fin comprises about 30 fin rays, mostly segmented two or three times. Most lepidotrichia branch distally. There are no fringing fulcra along the leading margin of any fin.

In three of the specimens, gastric residuals have been observed: besides the arguably predated *Paralepidotus*, the largest CGW specimen (Fig. 14) contains a pellet of fecal matter. A *Pholidophorus* fossilized in the stomach

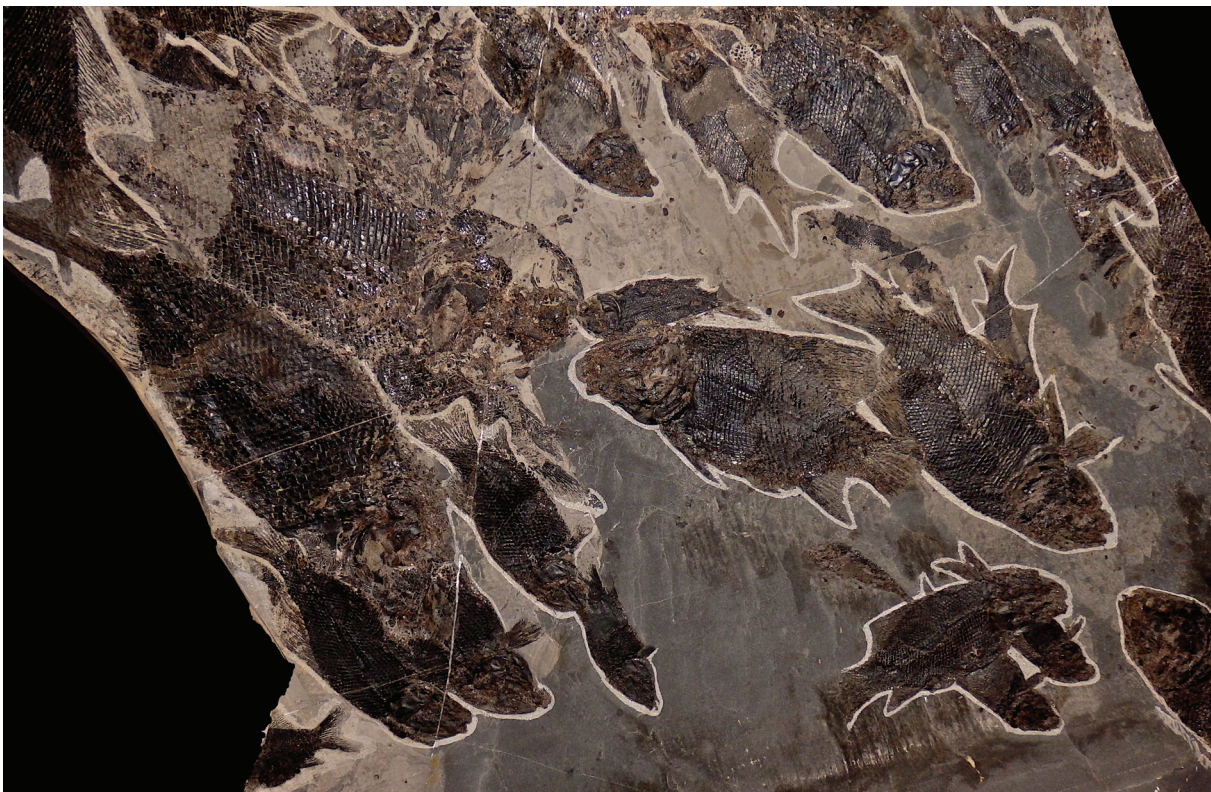


Figure 12: Large-sized plate (width ca. 50 cm, CGW) with showing different growth stages of *Paralepidotus*. Most of the fish bodies are oriented parallel to their longitudinal axis.

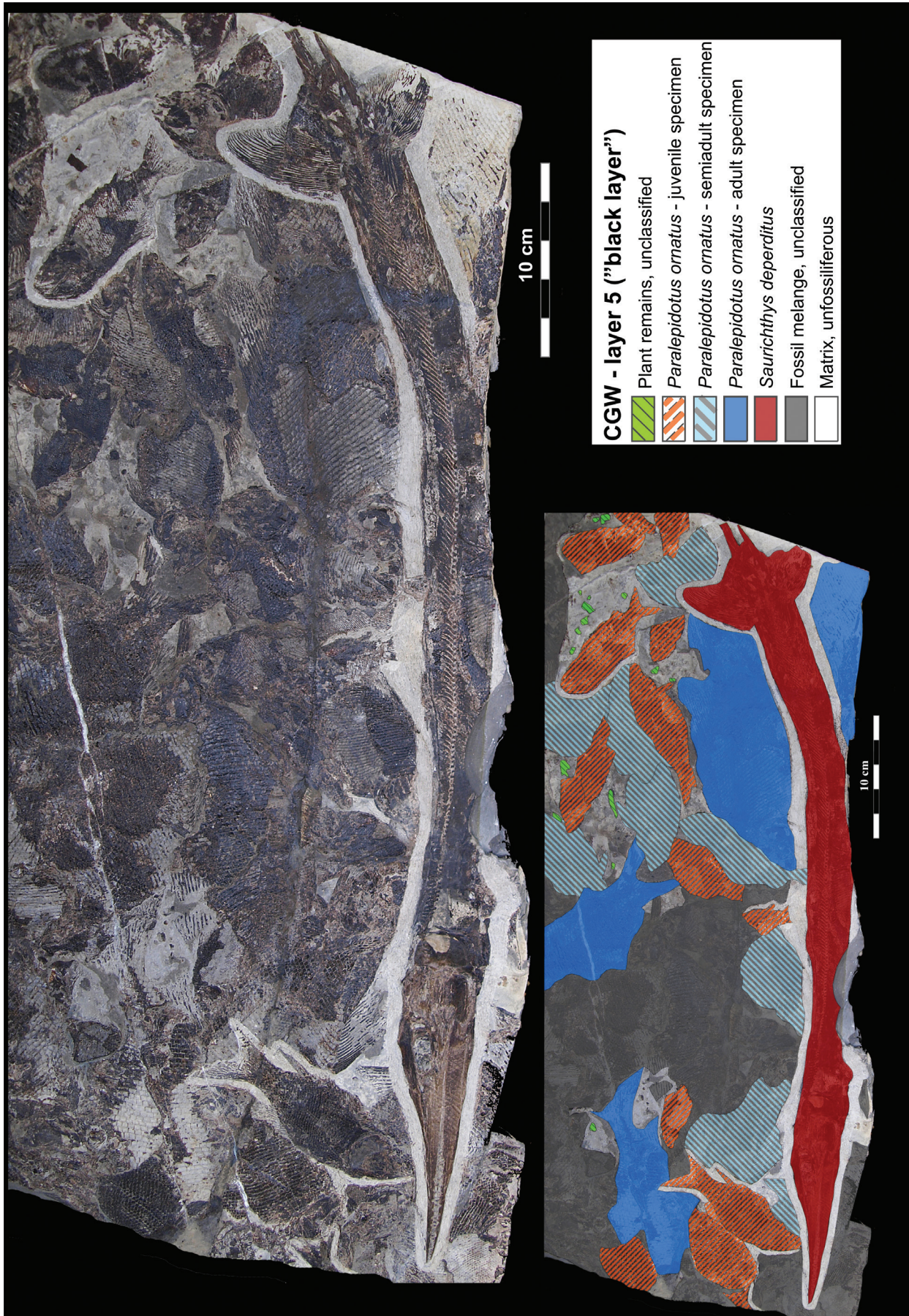


Figure 13: Large-sized plate (ca. 75 cm, CGW) with numerous superimposed, randomly arranged *Paralepidotus* as well a specimen of *Saurichthys deperditus* with soft part preservation (details are presented in Figure 14). The caudal fin of the latter specimen is not preserved.

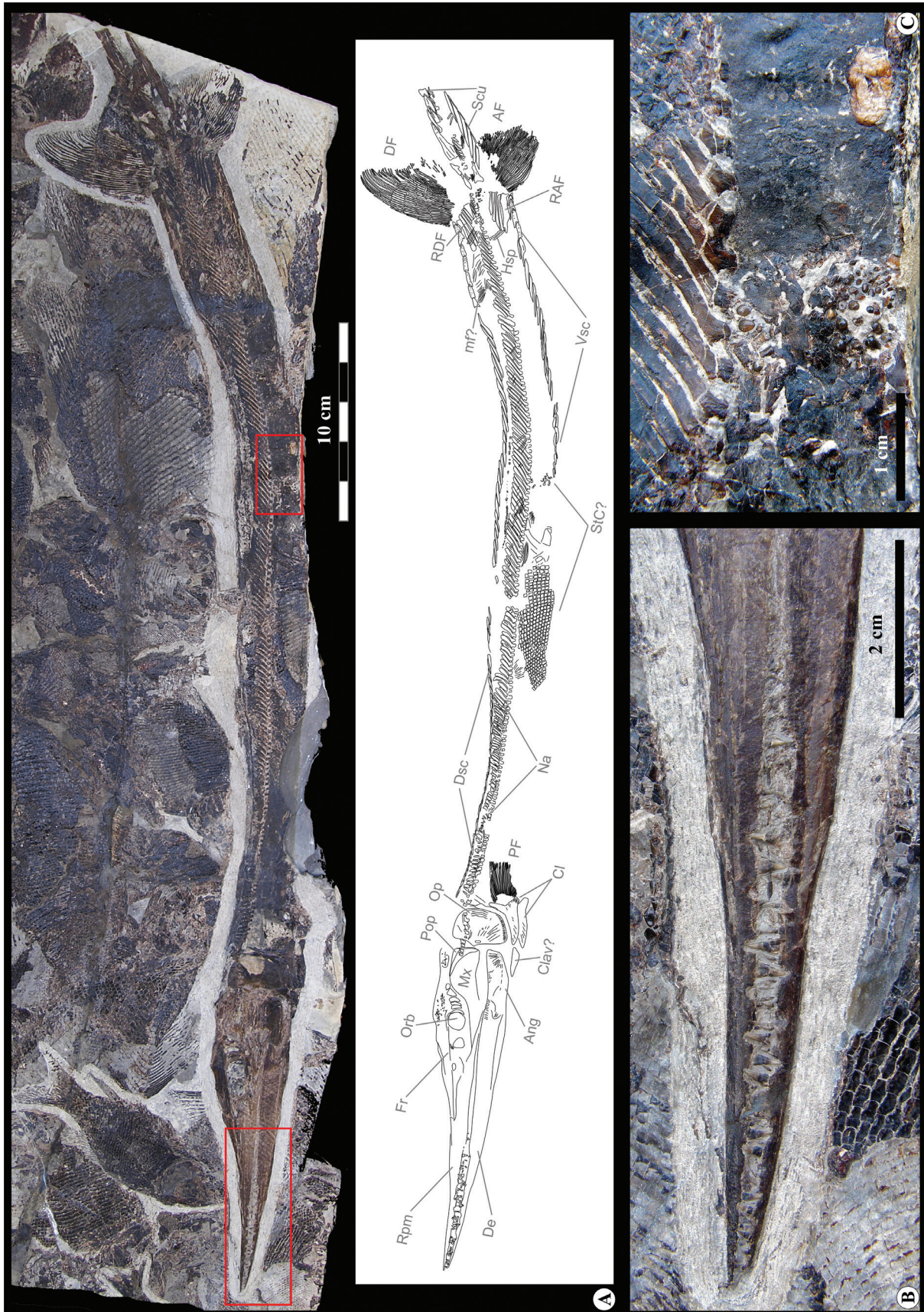


Figure 14: A) *Saurichthys deperditus* (Costa, 1862) (compare with figure 13) with a small *Paralepidotus ornatus* as possible stomach content. The sketch below illustrates the anatomical elements. Abbreviations: AF, anal fin; Ang, angular; Cl, cleithrum; Clv, clavicle; De, dentary; DF, dorsal fin; Dsc, mid-dorsal scales; Fr, frontal; Hsp, haemal spines; mf, muscle fibres; Mx, maxillary; Na, neural arches; Op, opercle; Orb, orbit; PF, pectoral fin; Pop, preopercle; RAF, radials of anal fin; RDF, radials of dorsal fin; Rpm, rostro-praemaxilla; StC, stomach content; Scu, precaudal scutes; Vsc, mid-ventral scales. B) Close-up of the jaws with characteristic saurichthyid dentition. C) Close-up of the mid-body area (red box in A) with teeth of the presumably predated *Paralepidotus ornatus* and a gastric residual (CGW).

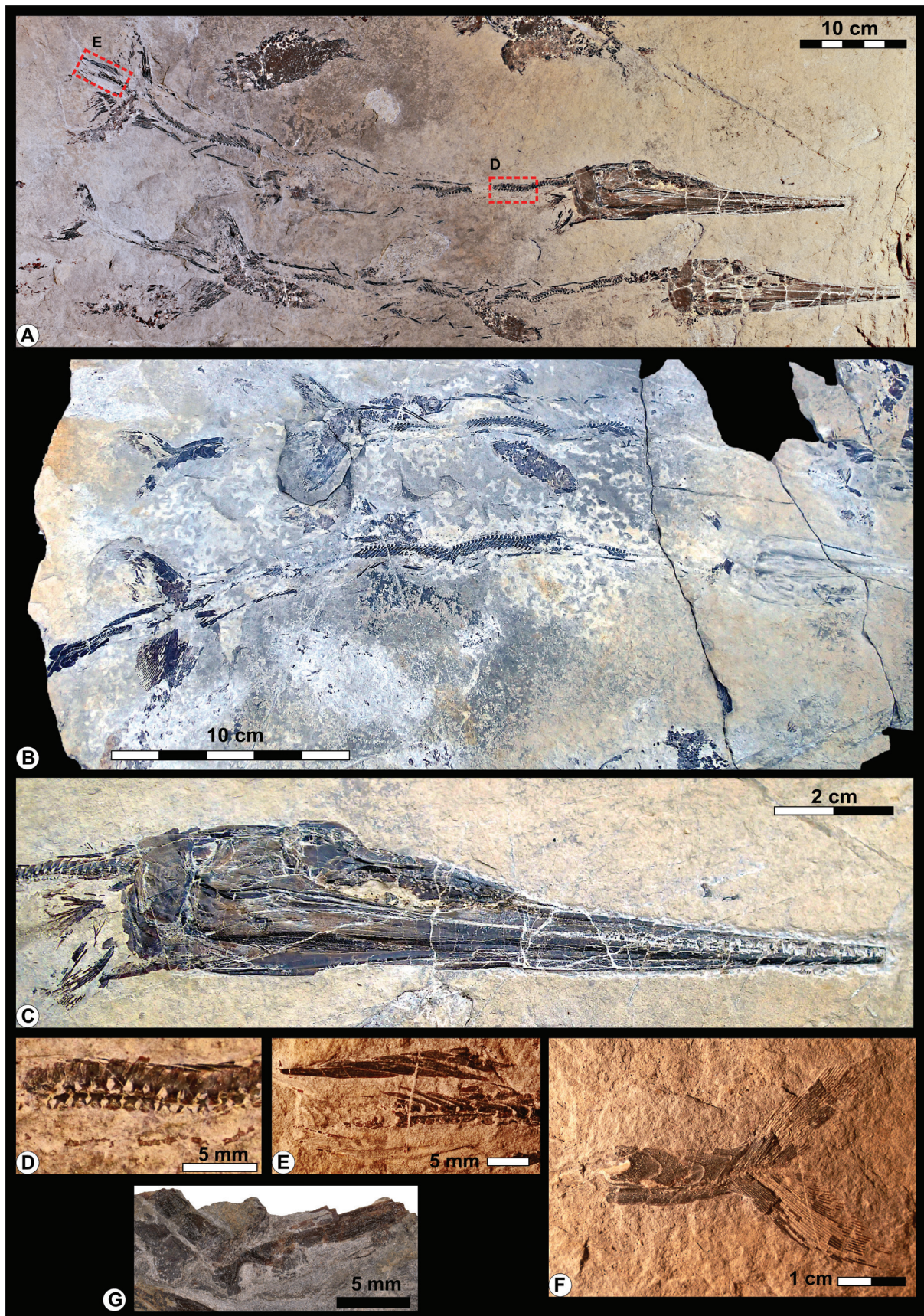


Figure 15: In the aftermath of our excavation campaign in autumn 2015, two unknown fossil diggers found a large-sized plate containing two isoorientated *Saurichthys deperditus* (Costa, 1862) in part (A) and counterpart (B). The lower specimen measures 440 mm, the upper one, lacking the caudal fin, 420 mm. This specimen has the better-preserved skull (C) and parts of the vertebral column (D: pectoral region; E: caudal region), while the caudal peduncle and fin (F) is well-preserved on the counterplate. A mid-body neural arch with praezygapophysis (pointing left) and neural spine (pointing right) is shown in picture (G). (CGW).

area of the lower CGW individual of Figure 15 is interpreted as prey due to its position and the distortion of the mid-ventral scale row and the vertebral column around it (probably caused by decay gases). And, finally, the unfigured CBG specimen exhibits an elongated, narrow, seemingly spirally wound yellowish structure ending at its anal opening, which can be identified as a cololite.

Neopterygii Regan, 1923

Infraclass **Holostei** Müller, 1845

Division **Ginglymodi** Cope, 1871

Order **Semionotiformes** Arambourg and Bertin, 1958

Family **Macrosemiidae** Thiollière, 1858

Genus **Legnonotus** Egerton, 1855

Legnonotus krambergeri Bartram, 1977

Figure 16A, B

1905 *Ophiopsis attenuata* – Gorjanović-Kramberger: 218, Pl. XX(IV) Figs 3, 4.

1977 *Legnonotus krambergeri* – Bartram: 164, Figure 20.

1983 *Legnonotus krambergeri* – Tintori and Renesto: Pl. 15, Figs 1, 2

2004 *Legnonotus cf. krambergeri* – Bürgin and Furrer, p. 75 ff.

Locus typicus: Wiestal, NE Hallein, Salzburg (Austria)

Stratum typicum: Seefeld Member, Upper Triassic

Holotype: British Museum, Natural History P10287.

Remarks: This small-sized but characteristic macrosemiid fish was described from the Wiestal as *Ophiopsis attenuata* (Gorjanović-Kramberger, 1905). Bartram (1977) formally erected the new species *Legnonotus krambergeri*, proposed in a handwritten catalogue by A. S. Woodward, based on original material from the “Hirtenstein Quarry” (Holotype P10287 in the British Museum of Natural History, London) as one of the earliest known, Norian-aged macrosemiid forms. Tintori and Renesto (1983) described the earliest macrosemiid fish *L. obtusus* from Carnian-aged rocks near Varese (Lombardy) and Bartram (1977) the species *L. cothamensis* from the Rhaetian of Gloucestershire (GB). The species of *L. krambergeri* was revised in detail by Tintori and Renesto (1983) based on new material from an Upper Norian limestone succession of Cene, Brembilla and Zogno (Lombardy, N’ Italy).

Material: Nearly 200 complete specimens from the fish layer 2 (bed 6; CTH, CGW), two specimens from fish-layer 3 (bed 5; CTH) as well as approximately 30 specimens embedded in swarms of fish-layer 4 (bed 4; CTH).

Description: *Legnonotus krambergeri* is a small-sized, slender neopterygian fish with an average length of 4 to 9 cm. The tapered, triangular skull shows a relatively large orbital opening. The frontal is ornamented with very fine scattered ganoine tubercles. *Legnonotus krambergeri* shows characteristically small, very slender teeth, of which 13 are arranged on the maxilla. Comprising a fine gap in-between, five slightly larger and more powerful teeth were positioned on the praemaxilla.

The most conspicuous attribute is the high and long undivided dorsal fin consisting of about 25 rays. The first

ray is the longest and is followed by rays gradually decreasing in length. The anal fin consists of seven rays. The caudal fin has a clearly forked outline, with an upper lobe of five rays and a lower lobe of eight rays. The paired pectoral fins show about 14 rays, the small distally elongate pelvic fins are made up of five rays at which both the basal and fringing fulcra are present.

The scales are rectangular and higher than long, pectinated at their posterior edges, becoming smaller towards the tail. The base of the dorsal fin is devoid of scales.

Family **Callipurbeckiidae** López-Arbarello, 2012

Genus **Semiolepis** Lombardo & Tintori, 2008

Semiolepis brembanus Lombardo and Tintori, 2008

Figure 17

1905 *Semionotus Kapffi* – Gorjanović-Kramberger: 196, Pl. XVIII (II), Figure 2.

2008 *Semiolepis brembanus* – Lombardo and Tintori: 131, Figures 1–8.

Locus typicus: Poscante-Zogno (Calcare di Zorzino; Lombardy, Northern Italy)

Stratum typicum: Middle / Late Norian boundary “vertebrate level” between Calcare di Zorzino and the Argillite di Riva di Solto

Holotype: MPUM 9288 Paleontological museum of the University of Milano

Remarks: Lombardo and Tintori (2008) described the new semionotiform genus and species *Semiolepis brembanus* from the Late Triassic of Italy. The authors included the only specimen of *Semionotus kapffi* reported by Gorjanović-Kramberger (1905) in the new taxon based on the illustration given in the original publication since the fossil could not be located in the collection of the University of Leoben since the year 2005.

Material: One moderately preserved specimen from fish-layer 3 (bed 5, CTH; see also Fig. 9) and three well-preserved specimens from fish-layer 4 (bed 4, CJW, CTH).

Description: *Semiolepis brembanus* is a fusiform neopterygian fish whose maximum body height is about mid-way between skull and dorsal fin. The frontal bone is flat, as opposed to the slightly arcuate one of *Paralepidotus*. Therefore, the complete skull looks more conical. Beyond that, all bones and scales are completely smooth and show no ornamentation.

The prominent but relatively small dorsal fin is placed posteriorly and preceded by a series of dorsal ridge scales with pronounced spines. It is situated at the level of the 24th transversal scale row and shows 14 lepidotrichia. They are not as widely spaced as described from the holotype by Lombardo and Tintori (2008), but the complete dorsal fin seems to be somewhat squeezed as a diagenetic consequence of circumstances during embedding.

The prominent spines on the dorsal ridge scales increase in length caudally, the posteriormost spines leading over to the fringing fulcra of the dorsal fin.

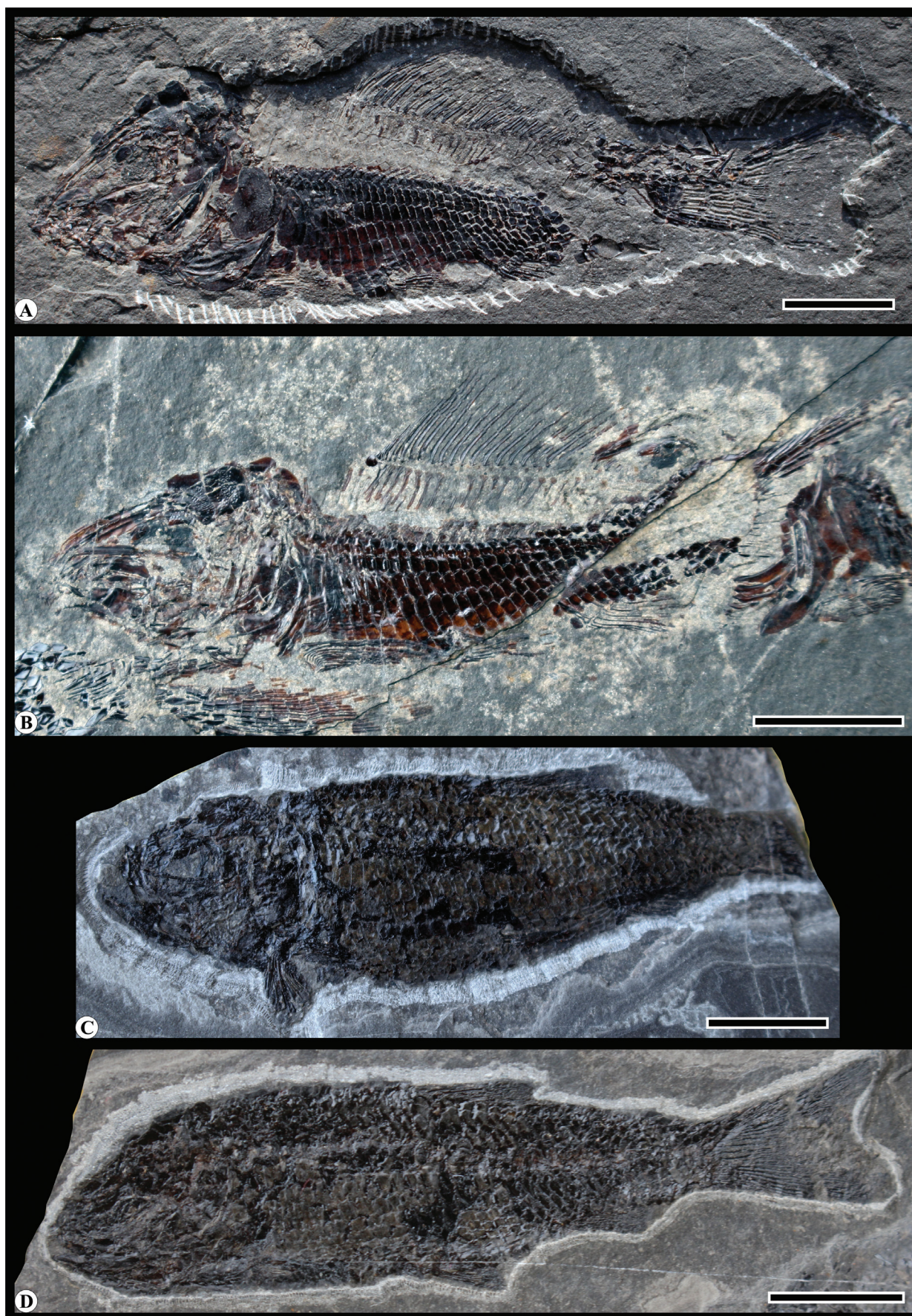


Figure 16: A) *Legnonotus krambergeri* Bartram, 1977 (bed 6, fish-layer 2), S.L. = 77 mm; B) *L. krambergeri* Bartram, 1977 (bed 6, fish-layer 2); S.L. = 57 mm; C) *Pholidophorus latiusculus* Agassiz, 1832 (bed 6, fish-layer 2); S.L. = 60 mm; D) *P. latiusculus* Agassiz, 1832 (bed 6, fish-layer 2); S.L. = 64 mm. Scale bars equal 10 mm. (All specimens CTH).

The anal fin begins at the level of the 19th transverse scale row and is smaller than the dorsal fin, showing eight lepidotrichia that are branching at least twice. As in the holotype in Lombardo and Tintori (2008), elements of basal fulcra can be observed.

The caudal fin consists of 20 lepidotrichia framed by basal and fringing fulcra at the fin margins. A segmentation count as given in the original description of Lombardo and Tintori (2008) cannot be provided due to the incomplete preservation of the specimen pictured in Figure 17A.

The squamation consists of 35 vertical and 21 horizontal scale rows that all show all a smooth surface without ganoine ornamentation. The anteriorly situated scales

of the latero-ventral flank are high-rectangular – their height decreases towards the posterior flank. Here, most scales have a strictly rhombic shape.

Genus ***Paralepidotus*** Stolley, 1920

Paralepidotus ornatus (Agassiz, 1834)

Figures 18, 19

1833 *Lepidotus ornatus* – Agassiz: Tome II, Pt. 1: 9 (1. livraison).

1834 *Lepidotus ornatus* – Agassiz: Atlas Tome II, Pl. 32 (2. livraison).

1837 *Lepidotus ornatus* – Agassiz: Tome II, Pt. 1: 249 (8./9. livraison).

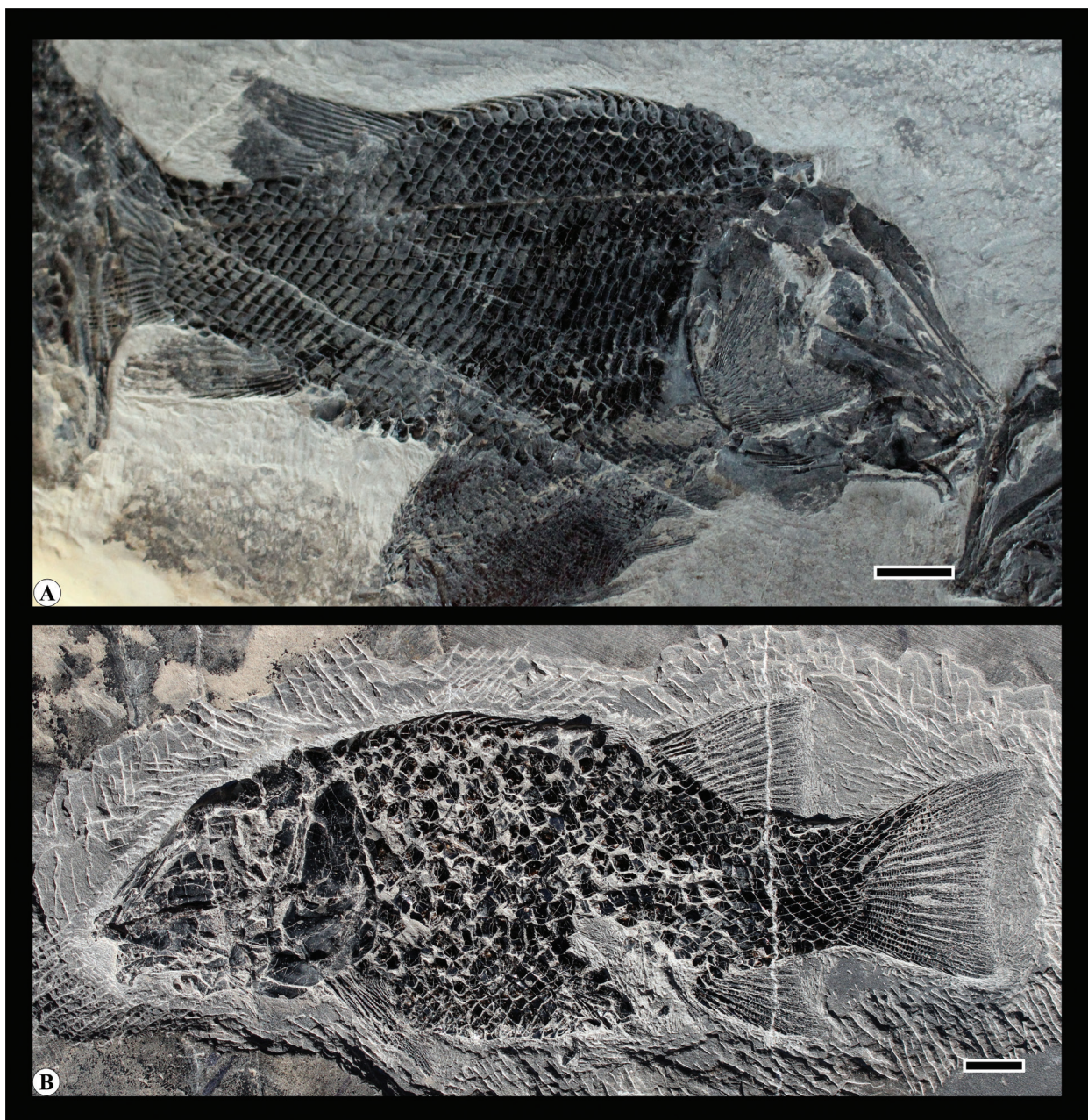


Figure 17: A) *Semiolepis bremanus* Lombardo and Tintori, 2008 (bed 4, fish-layer 4; CJW), S.L. 119 mm. B) *S. bremanus* Lombardo and Tintori, 2008 (bed 4, fish-layer 4; CJW) showing a partly disarticulated region anterior to the anal fin, S.L. = 157 mm. Scale bars equal 10 mm.

1892 *Lepidotus* [*Colobodus*?] *ornatus* – Bassani: 17.
 1896 *Colobodus ornatus* – Bassani: 187, Pl. XII Figure 8,9, Pl. XIII Figure 1, Pl. XIV, Pl. XV Figure 4–30.
 1905 *Colobodus ornatus* – Gorjanović-Kramberger: 199, Figure 2–8, Pl. XVII (I) Figure 1, Pl. XVIII (II) Figure 1, Pl. XXI (V) Figure 1, 4.
 1905 *Colobodus elongatus* – Gorjanović-Kramberger: 208, Figure 9–11, Pl. XIX (III) Figure 1.
 1905 *Colobodus (Lepidotus) decoratus* – Gorjanović-Kramberger: 210, Pl. XVII (I) Figure 2.
 1905 *Heterolepidotus dorsalis* – Gorjanović-Kramberger: 212, Figure 12, Pl. XIX (III) Figure 2, 3, Pl. XX (IV) Figure 1.
 1905 *Heterolepidotus parvulus* – Gorjanović-Kramberger: 214, Figure 13, Pl. XX (IV) Figure 2.
 1920 *Paralepidotus ornatus* – Stolley: 41.
 1988 *Paralepidotus ornatus* – Tintori and Olivetti: 39, Figures 1–4.
 1996 *Paralepidotus ornatus* – Tintori: 171, Figures 1–6.

Locus typicus: Seefeld (Tyrol, Austria)

Stratum typicum: „bituminous shales“ of the Norian, Upper Triassic.

Holotype: “Societe Geologique de France” or Museum of Natural History, Stuttgart (Schultz 2013: pp. 152).

Remarks: Agassiz (1833–1843) originally erected the species as *Lepidotus ornatus* based on poor and incompletely preserved material from Seefeld. As Tintori (1996) noted, the specimens pictured by Agassiz are lost, but due to the description and the illustration showing some distinctive features (as, for instance, the shape of the cheek bones, the scale ornamentation, the large size, etc.), he considered the designation of a neotype as unnecessary (!). Many specimens were recovered during the end of the 19th century from different, coeval sites, classified under new taxa (see Tintori, 1996). Bassani (1892, 1896) assigned the finds to the genus *Colobodus*, based mainly on dental features. Following this concept, Gorjanović-Kramberger (1905) described specimens from the Wiestal “Hirtenstein Quarry” as *Colobodus ornatus* (for mid-sized fishes), *C. elongatus* (for larger forms with a dorsal hump), *C. (Lepidotes) decoratus* (for a single squamation fragment), and smaller ones under the name *Heterolepidotus dorsalis* and *H. parvulus*. Andersson (1916) stated that *C. ornatus* should be excluded from *Colobodus* because of obvious osteological differences. Taking this into account as well the geographic and stratigraphic distribution of the species (Germanic Middle Triassic [“Muschelkalk”] for *Colobodus* vs. Alpine Late Triassic for the Wiestal form), Stolley (1920) erected the genus *Paralepidotus*, which he considered close to *Lepidotes*; the morphology and ontogeny of this taxon, however, remained little-known until Tintori’s (1996) concise revision. Based on the immense material, Tintori (1996) documented a series of ontogenetic transformations within individuals of the only species *Paralepidotus ornatus* that accounted for the considerable variation in size, body outline, the size and relative position of fins, dentition and scale ornamentation, that, in turn, can be

correlated with habitat and dietary changes (see also Lombardo and Tintori, 2005).

Material: Several hundred specimens of different growth stages (4 to 87 cm S.L.) found throughout the complete excavated section (bed 1 to bed 9), embedded isolated and in swarms. About 70% are juveniles, followed by 25% subadults. Adult individuals account for only ca. 5% of the material and are usually restricted to single occurrences, although up to three large fishes on the same bedding plane within one square meter have been excavated from fish layer 3.

Description: The high number of well-preserved specimens found in all fish layers allows the observation of different growth stages of this highly variable species. A highly detailed anatomic description of the skull and the postcranial skeleton is given by Tintori (1996). The specimens pictured in this context as well as the majority of specimens of the genus *Paralepidotus* we found during our excavations correspond exactly to this description.

Juvenile and subadult growth stage (Fig. 18A,B; 19A,B,C): The juvenile and subadult stages of *Paralepidotus ornatus* differ from adults in many aspects and may explain the past nomenclatural confusion about this taxon. The average size of juvenile *Paralepidotus* is about 4 to 10 cm (Fig. 18A), the subadult stage reached 25 cm (Fig. 19C). The small specimen pictured in Figure 18A shows a relatively large skull followed by a slender body that narrows consistently towards the caudal fin. The body shape of the somewhat larger specimen in Figure 18B is deeper, showing its highest point between the skull and the onset of the dorsal fin.

In all small-sized specimens, the most conspicuous skull bone is the large, rectangular, completely smooth opercle, whose boundaries to the subopercle, the cleithrum, and the branchiostegal rays are very faint. This large bone bends towards the prominent dentary, which is hinged down presenting the gaping mouth with small, slender and high-crowned teeth, each of which shows an apical tubercle. The large orbital opening is reduced and acute-angled beneath the crenulated, flat and even frontal bone and is surrounded by seemingly fused, rounded and very small supraorbital and infraorbital elements.

The scales of the body flank are of high-rectangular shape, decreasing in height towards posteriorly and being of rhomboid shape directly before the onset of the caudal fin. In contrast to the subadult and adult growth stages, they are completely smooth and show no ornamentation. The pectoral fin is long and slender, with 16 lepidotrichia. The pelvic fins of the specimen of Figure 18A are not visible; the specimen in Figure 18B exhibits each six pelvic lepidotrichia. The relatively small dorsal fin of both figured specimens has a symmetrical-triangular shape with a prominent “central peak”. This “peak” is formed by the second or third, longest lepidotrichium that is situated posterior to a faint series of fringing fulcra. The lepidotrichia following the longest ray gradually decrease in length towards the caudal peduncle (Fig. 19B); about 27 dorsal fin rays can be counted in this specimen.



Figure 18: Different growth stages of the anatomically highly variable species *Paralepidotus ornatus* (Agassiz, 1834; A) juvenile specimen, S.L. = 60 mm (bed 4, fish-layer 4; GJW); B) subadult specimen, S.L. = 134 mm (isolated specimen from bed 7; CTH); C) adult specimen, S.L. = 263 mm (bed 5, fish-layer 3; CTH); D) adult, very large-sized specimen, S.L. = 872 mm (bed 5, fish-layer 3; CJW).

The anal fin has a similar shape to the dorsal fin but is considerably smaller, consisting of only 12 to 13 rays.

The caudal fin of both specimens consists of 23, centrally partly well-spaced rays that start to fan out in the larger specimen of Figure 18B. In both specimens, there are two or three basal and fringing fulcra.

Adult growth stage (Figs. 18C, 18D, 19D): As mentioned above, the body shape of the rare adult and the very large-sized, so-called “senile” specimens is considerably

deeper, often showing a more or less significant hump anterior to the dorsal fin (Fig. 19D).

Regarding the skull, the arrangement of bones is not much different compared to the juvenile and subadult specimens. Differences consist in the strong ornamentation of the opercle, praeopercle, supracleithrum and the anterior part of the dentary. In addition, the skull of the specimen in Figure 18D reveals that also some of the infraorbital and supraorbital bones may be ornamented.

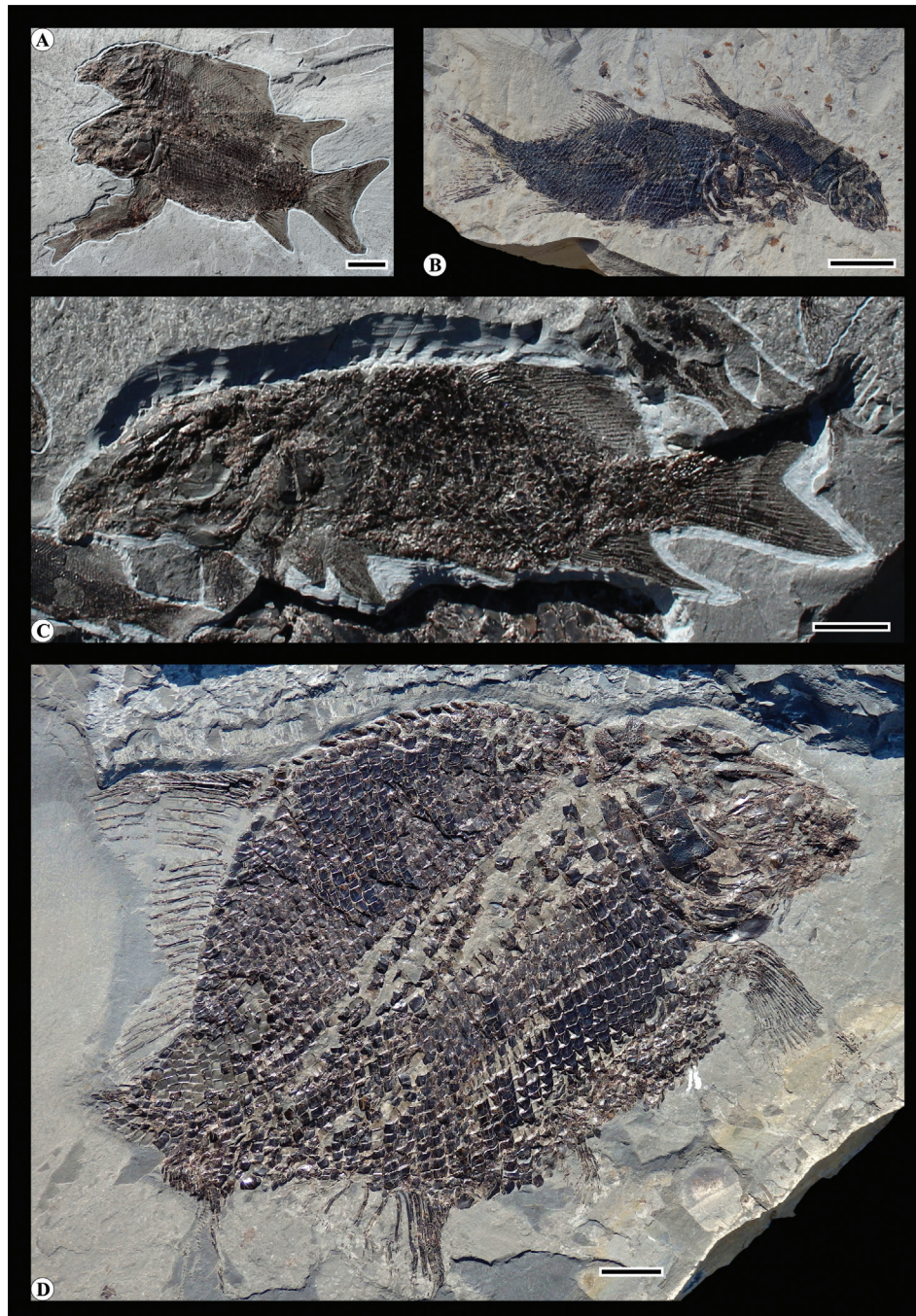


Figure 19: Different shapes of the anatomically highly variable species *Paralepidotus ornatus* (Agassiz, 1834): A) Group of two typically shaped fusiform subadult and one slender juvenile specimen (S.L. of the large specimen = 162 mm; isolated found in bed 7; CTH); B) Two subadult specimen of the weathered surface of bed 9 (fish-layer 1; S.L. of the large specimen = 115 mm) with plant remains (CGW); C) Unusual slender subadult specimen showing a rather more posterior insertion of the dorsal fin (S.L. = 231 mm bed 6, fish-layer 2; CTH); D) Hump-back shaped adult specimen from bed 5 (fish-layer 3; S.L. = 261 mm). Scale bars equal 20 mm.

Most conspicuously, the shape of the teeth has changed from the above-mentioned high-crowned, slender teeth of juvenile growth stages to low, hemispherical, knob-like teeth showing a completely smooth occlusal surface (Fig. 20).

Similar to the dentition, also the appearance of the scales changes ontogenetically: juvenile individuals (Fig. 18A) show small, smooth scales with a ganoine layer. The scales of the anterior and mid-body flank of the specimen pictured in Figure 18C show two longitudinal ridges. In the specimens in Figures 18B, 18C and 19C, scales with small tubercles, which are very similar to the ornamentation of the aforementioned skull bones, predominate. The crenulation of the scale surfaces disappears farther caudally on the body, but persists on the dorsal flank beneath the dorsal fin. The number of longitudinal sculpture ridges, as described from the subadult specimens (Fig. 18C), increases up to 10. The very large fish in Figure 18D exhibits crenulated scales on the dorsal part of the body flank, scales with longitudinal ridges in the ventral part of the flank and smooth scales in the dorsal part of the caudal peduncle.

Compared to juvenile *Paralepidotus*, the origin of the dorsal fin is shifted forward, and its outline has changed from a triangular shape to rounded, craned towards posterodorsally. The pectoral fin of adult specimens is widened and fan-shaped, with 16 to 17 strong lepidotrichia preceded by a large basal fulcrum. The small pelvic fins consist of five rays, with a series of fringing fulcra along the leading margin. The dorsal fin contains 25 long, bifurcating rays preceded by basal and fringing fulcra. The anal fin includes 14 to 15 lepidotrichia. The large caudal fin shows 24 lepidotrichia and conforms to the observations of Schultze and Arratia (1989) with one dorsal procurent, 20 principal rays and three ventral procurents, framed by some basal and a tight series of fringing fulcra. All rays are ornamented in a plait-pattern. The rays are more widely spaced towards the center of the dorsal fin. Similar to the dorsal and anal fins, the rays of the caudal

fin are fanned out towards their distal end, creating a very fine and flexible web.

Order Dapediiformes Thies and Waschke, 2016

Family **Dapediidae** Lehman, 1966

Genus ***Dandya*** White and Moy-Thomas, 1941

Dandya ovalis (Gorjanović-Kramberger, 1905)

Figure 21

1905 *Spaniolepis ovalis* - Gorjanović-Kramberger: 217, Figures 15, 16, Pl. XX (IV), Figures 6–8.

1941 *Dandya* - White and Moy-Thomas: 399.

1983 *Dandya ovalis* - Tintori: 430, Figure 3, Pl. 37, Figure 2.

Locus typicus: Wiestal, NE Hallein, Salzburg (Austria)

Stratum typicum: Seefeld Member in the Hauptdolomit, Norian, Upper Triassic

Syntypes: GIMLeoben 6920 (old number 1562) – original to Gorjanović-Kramberger (1905).

Remarks: The taxon described as *Spaniolepis ovalis* by Gorjanović-Kramberger (1905) from the “Hirtenstein Quarry” has been renamed *Dandya* by White and Moy-Thomas (1941) for formal reasons. Tintori (1983) gave a detailed redescription of the species based on new material from Zogno, Ponte Giurino and Cene (Lombardy, Northern Italy).

Material: Two incomplete (broken) specimens from bed 6 (fish-layer 2, CGW, CTH). Both specimens show a moderately preserved skull and axial skeleton but lack the posterior part of the dorsal and anal fin as well as the complete caudal fin.

Description: As mentioned above, most of the skeletons of small-sized ganoid fishes found in bed 6 (fish layer 2), are preserved wafer-thin without solid contact to the matrix. In addition, our specimens of *Dandya ovalis* (Figs. 21A, B) have been partly torn apart. Thus, the skull shows only some characteristic features described before by Tintori (1983): the frontal is broken but seems to be a rather strong and smooth, sculptureless

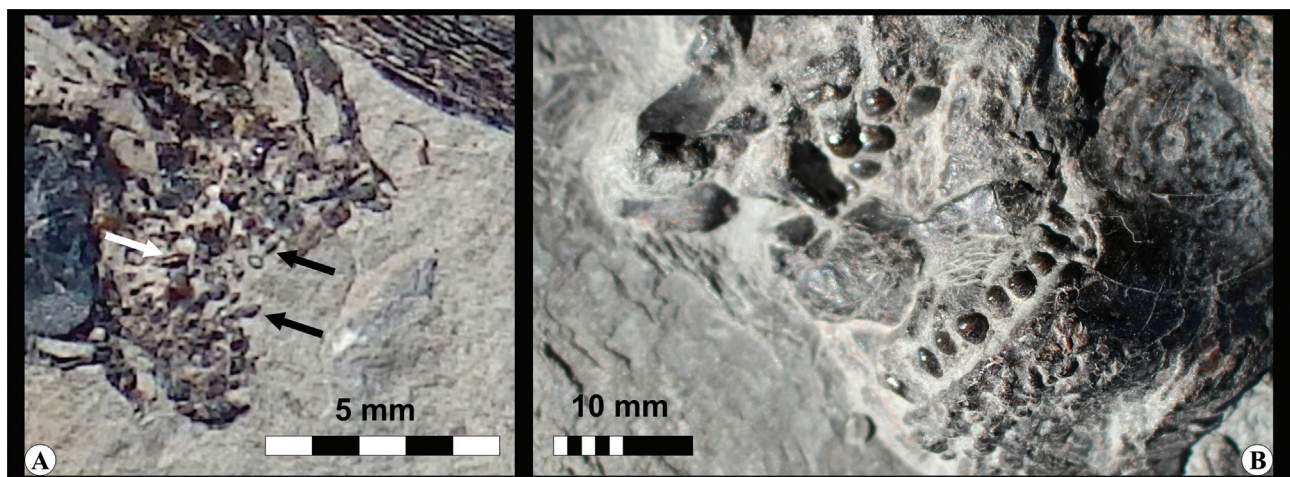


Figure 20: Ontogenetic changes in the dentition of *Paralepidotus ornatus* (Agassiz, 1834): A) pointed, slender teeth of the juvenile individual from Fig. 19B (black and white arrows); B) hemispherical knob-like teeth with a smooth occlusal surface of the adult individual from Fig. 18D.

roof-bone situated dorsal to the relatively large eyehole. The opercle is preserved only as an impression, but it is very high, at least twice its length. The maxilla beneath is edentulous and slender anteriorly, strengthening towards its posterior end. The praemaxilla is not clearly visible, even the dentition, respectively the number of teeth is unclear. The crescent-shaped, rather robust dentary holds five very slender pointed teeth at its anterior end. The squamation is incomplete, restricted to small scales near the dorsal mid-line, behind the pelvics and in front of the dorsal fin, which may, however, be a preservational effect. The axial skeleton is well visible, partly preserved in original bone substance, partly as an imprint. However, no vertebral count can be given due to the incompleteness of the specimens.

The paired pectoral fins are preserved only as a very fine impression and the number of lepidotrichia is unknown –

the small pelvic fins, which are situated rather posteriorly near the onset of the anal fin, consist of five long lepidotrichia. The dorsal fin is long-based, with at least 22 long endoskeletal radials supporting it, and begins more or less at the level of the pelvics. The anal fin, starting farther caudally than the dorsal fin, is too incompletely preserved to allow a description.

Order **Pycnodontiformes** Berg, 1937
incertae familiae

Genus **Eomesodon** Woodward, 1918
Eomesodon hoeferi (Gorjanović-Kramberger, 1905)
Figures 22, 23

1905 *Mesodon Hoeferi* – Gorjanović-Kramberger: 219,
Figure 17, 18, Pl. XX Figure 5, Pl. XXI Figure 2.
1918 *Eomesodon hoeferi* – Woodward: 54.

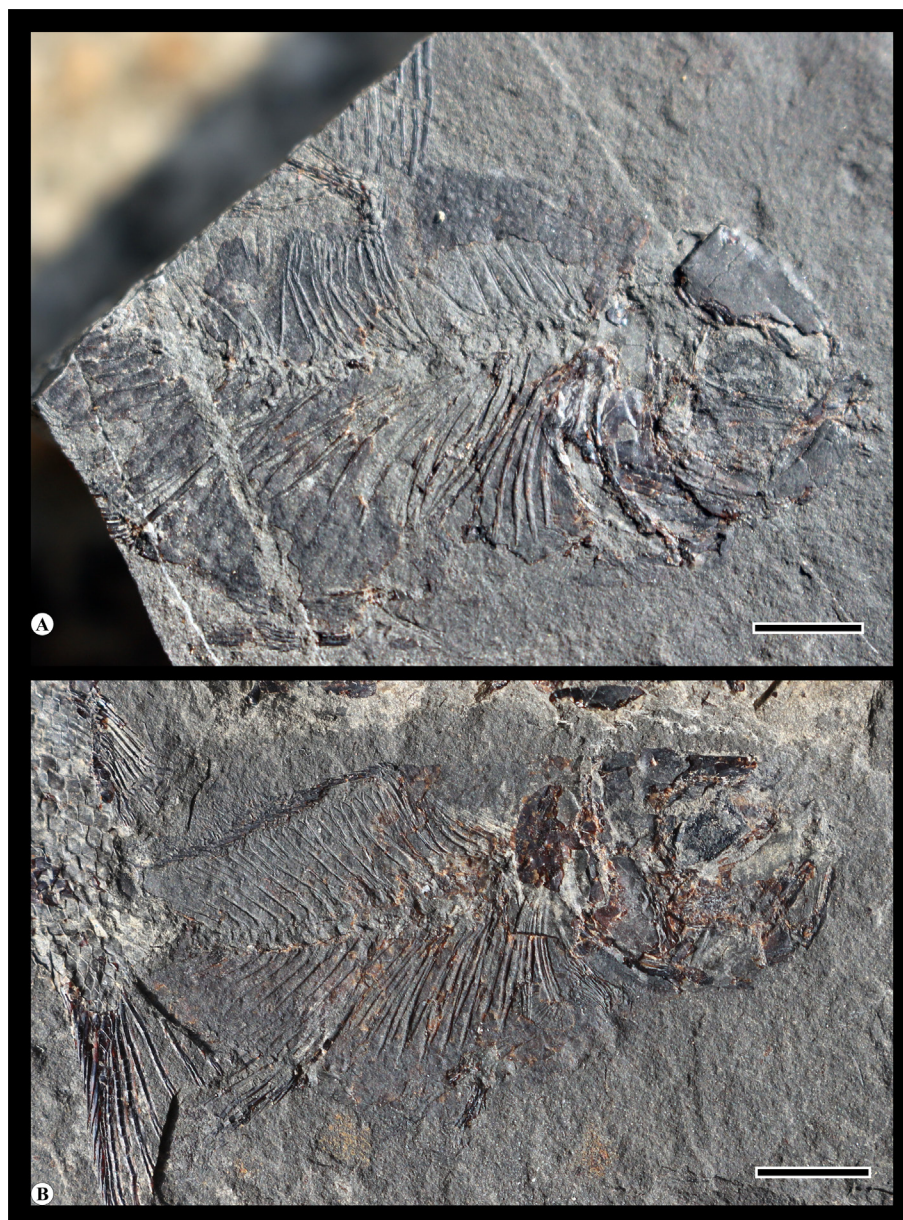


Figure 21: A) *Dandya ovalis* (Gorjanović-Kramberger, 1905) (bed 6, fish-layer 2; CGW), S.L. = 40 mm; B) *Dandya ovalis* (Gorjanović-Kramberger, 1905) (bed 6, fish-layer 2; CTH), S.L. = 36 mm; Scale bars equal 5 mm.

Locus typicus: Wiestal, NE Hallein, Salzburg (Austria)

Stratum typicum: Seefeld Member in the Hauptdolomit, Norium, Upper Triassic

Syntypes: GIMLeoben 6947 (old number 1555); GIMLeoben 6948; original to Gorjanović-Kramberger (1905).

Remarks: One of the two specimens reported by Gorjanović-Kramberger (1905) has been retrieved in the collection of the University of Leoben (Schultz and Piller 2013:144). The other, better-preserved individual from the type series, however, could not be located. Based on Gorjanović-Kramberger's (1905) illustration and description of this specimen, Poyato-Ariza and Wenz (2002) suggested that *E. hoeferi* is a juvenile form because of its very small size (23 mm) and weak ossification, i.a. of the fin rays. They recommended a revision of this species. Up to now, eleven specimens have been found at the Wiestal site since Gorjanović-Kramberger's (1905) description, two of which are stored at the University of Leoben (Schultz and Piller, 2013). The first of the more recent finds was made during the excavation campaign in 1993 and is stored in the Burgmuseum Golling (Salzburg, Austria). Eight additional specimens were found during this excavation. All our complete specimens are between 29 and 36 mm long (S.L.) and are pictured in this publication (Figs. 22, 23). Furthermore, we have found one incomplete, most probably juvenile specimen with a total length of 19 mm. Given this span of body sizes without significant osteological changes, we propose that these small-sized fishes do not represent a “juvenile”

growth-stage of a larger-sized gyrodonitid but rather a species that is fully grown with 40 mm total length and which has to be redefined in the future.

Eomesodon shows a very long-lasting stratigraphic range: besides our Norian findings, which are among the oldest known Pycnodontiformes, a piece of the lower dentition is known from the Rhaetian Kössen-Formation of the Schesaplana region (Vorarlberg, see Schultz and Piller, 2013:144). The genus occurs even very rarely within the lithographic limestones of the uppermost Jurassic of Southern Germany (Arratia et al., 2015: 129) as well as in the Jurassic-Cretaceous boundary interval of Dorset, United Kingdom (Poyato-Ariza and Wenz, 2002).

Material: Eight specimens from the excavation campaign of the years 2013 and 2014. The first specimen (number 1 in table 2 and Fig. 22A) was found in spring 2013 isolated within bed 2 (CGW). It shows a far better preservation than the specimens pictured in Gorjanović-Kramberger (1905). It is preserved on plate and counter-plate. Due to the moment of finding, pieces of the postcranial skeleton were torn apart; some very fine bone material was blistered (vertebrae, ribs as well as caudal and dorsal fin rays). The seven other specimens were found in the time span between April 2016 and April 2017 during preparation of stored hand rock samples of fish layer 2 of bed 6 (CGW, CTH). As all the actinopterygian fishes found in this horizon, they are moderately preserved (mostly) on plate and counterplate showing the wafer-thin body skeleton as well as, in most cases, the paired and unpaired fins.

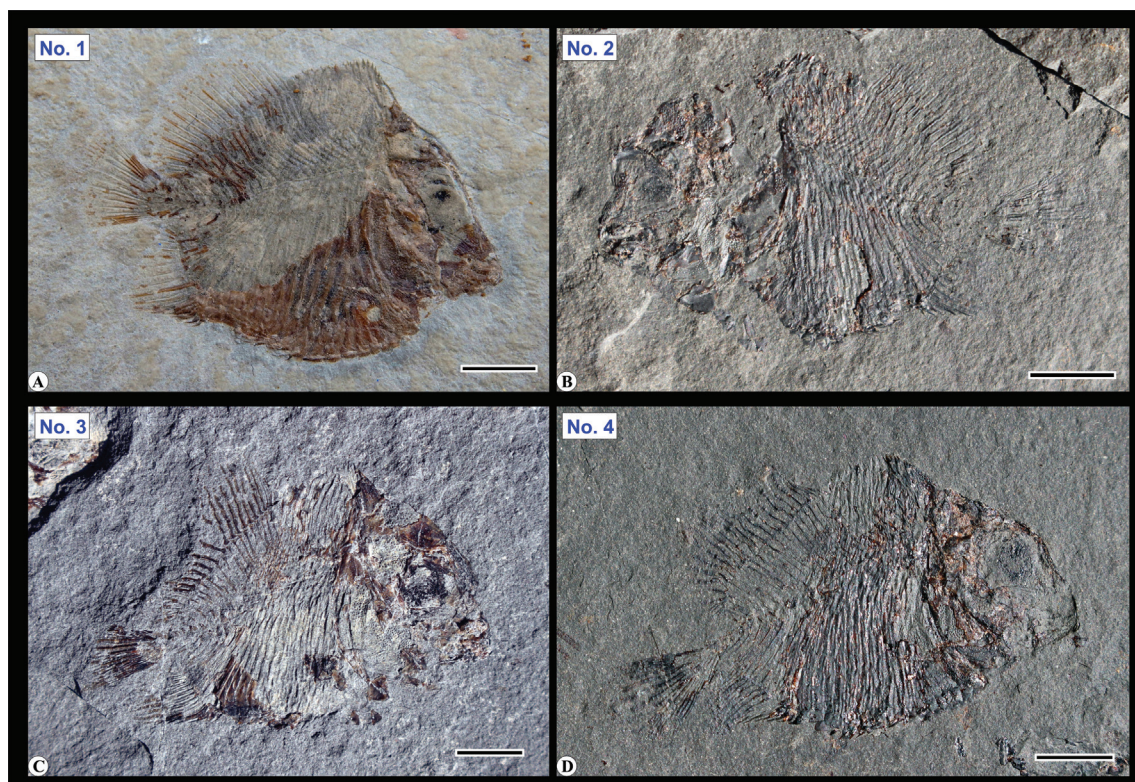


Figure 22: A) *Eomesodon hoeferi* Gorjanović-Kramberger (1905) (bed 2), S.L. = 29 mm; B) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 29 mm; C) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 36 mm; D) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 33 mm. Scale bars equal 5 mm.

Description: Most of the individuals found during the excavation are preserved on plate and counterplate (exception: specimen 8). Thus, parts of the skull as well as the caudal skeleton are incomplete or absent. Table 2 gives an overview of the specimens and their morphological characters relevant for biometric implications. All finds are between 19 mm and 36 mm long (S.L.) and show a round to oval shape.

The high and slim skull is blunt towards the jaws, showing a large eyehole. The majority of the pictured

specimens (Figs. 22A to D, 23B) demonstrate a blackish substance in the region of the large orbital opening, which we interpret as a remnant of the organic substance of the eye (soft-part preservation). A large preopercle and a high, triangular opercle are situated posterior to the orbit. Anteriorly, the frontal bone forms a very slim, straight and fracturable ridge. The frontal, opercular, praeopercular and subopercular bones are sculptured with a distinct granulation (Figs. 22A-D, 23A-B). The sculptured frontal bone of the specimen pictured in Figure 23C is dislocated

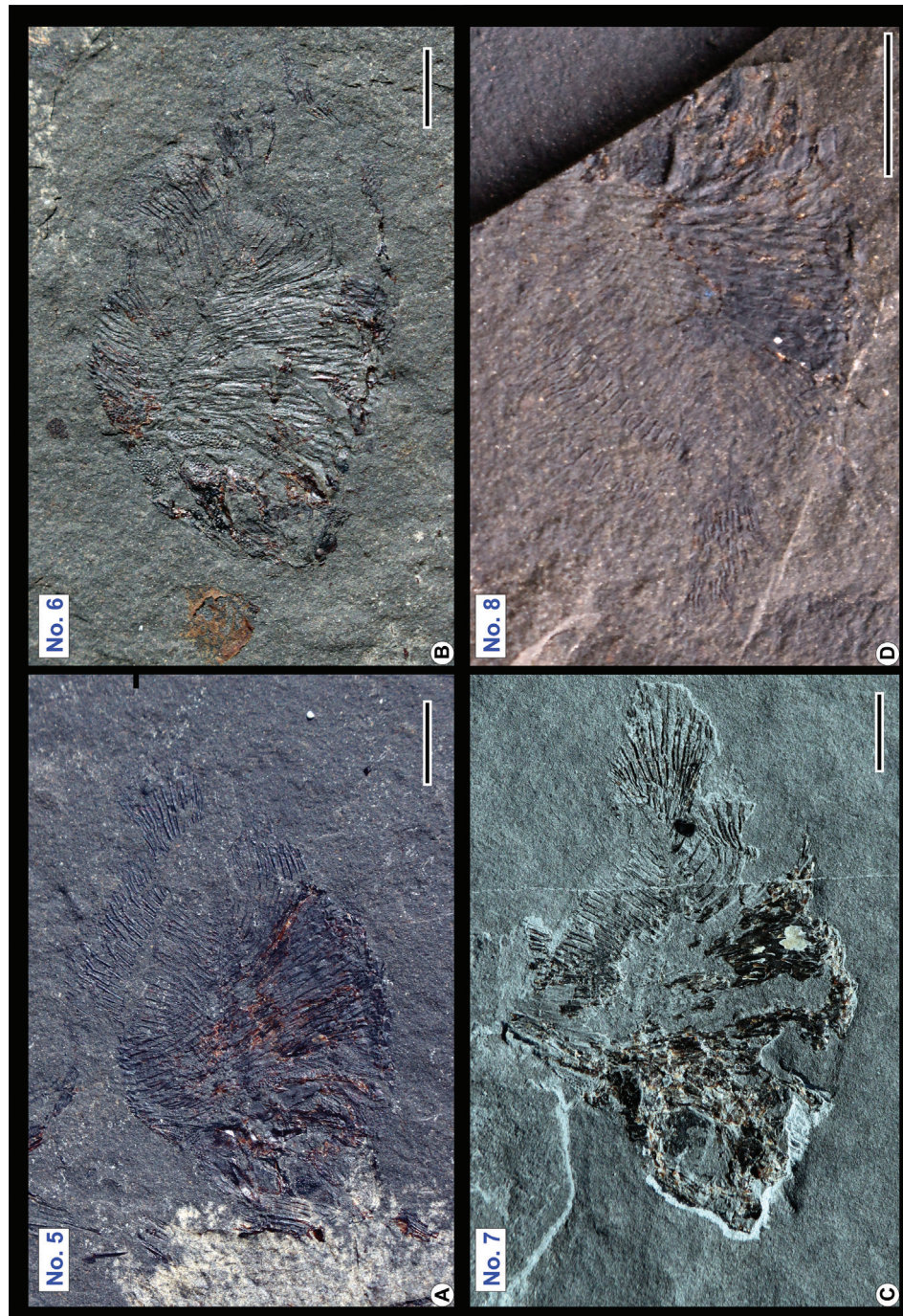


Figure 23: A) *Eomesodon hoeferi* Gorjanović-Kramberger (1905) (bed 2), S.L. = 31 mm; B) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 30 mm; C) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 36 mm; D) *E. hoeferi* Gorjanović-Kramberger (1905) (bed 6, fish-layer 2), S.L. = 19 mm; Scale bars equal 5 mm.

Number	Collection	Figure	Length [mm]	Height [mm]	Number of lepidotrichia				Number of Vertebrae
					caudal fin	anal fin	dorsal fin	pectoral fin	
1	CGW	22A	29	23	16	4	23	8	28
2	CTH	22B	29	20	16	n.v.	22	n.v.	n.v.
3	CTH	22C	36	22	16	4	23	8	27
4	CTH	22D	33	19	16	4	23	n.v.	27
5	CGW	23A	31	17	?16	4	22	8	n.v.
6	CTH	23B	30	18	n.v.	4	n.v.	n.v.	28
7	CGW	23C	36	22	16	4	22	n.v.	n.v.
8	CTH	23D	19	12	?14	4	22	n.v.	27

Table 2: Biometry of the eight collected specimens of *Eomesodon hoeferi* (Abbr.: CGW = collection Gerhard Wolf, CTH = collection Thomas Hornung; n.v. = not visible).

from of its anatomically correct position and displaced towards the dorsal fin, leading to a somewhat depressed, low-oval outline of the skull. The small specimen pictured in Figure 23D (main parts of the frontal bone are missing) is preserved only as a very delicate imprint showing main parts of the unpaired fins. The granulation of the skull bones as well as the dentition are not preserved.

As for the complete specimens, the dentition is well preserved and conforms to the description of Gorjanović-Kramberger (1905). The praemaxilla of the upper jaw exhibits a pair of slender front teeth, the proximal part of the dentary shows a single tooth of similar shape. The front teeth are slightly arched forward. Behind these, the upper and lower jaws bear at least five longitudinal rows of small, rounded teeth; the central row bears the largest teeth, their size diminishes towards the marginal rows.

The vertebral column consists of paired neural and haemal arches surrounding the persistent notochord. Long, arcuate neural and haemal spines branch off from the arcual elements at an angle of approximately 110° to the notochord in caudal direction, which changes to nearly 90° in the posterior body part. The vertebral count is about 26 to 28. The fine ganoid squamation is restricted to a triangular area spanned by the insertion of the dorsal fin, the pectoral fin and the anal fin (Gorjanović-Kramberger, 1905); the scales of the dorsal flank are rod-shaped in lateral direction, and the vertical scale-rows are not in contact with each other.

A steep dorsal projection of the skull roof gives way to a peculiar hump, which is clearly visible in all specimens pictured in Figure 22. The insertion of the dorsal fin is situated behind this hump somewhat in the middle of the axial skeleton, and the fin consists of 23 long rays. The first six to seven rays gradually increase in length, while the length of the following lepidotrichia gradually declines. The small last rays lead over continuously to short ridge scales and the caudal fin. The caudal fin consists of 16 short and densely arranged lepidotrichia. Their length increases from the dorsal and ventral margins towards the midline of the fin, so that its outline is clearly rounded and not forked. The anal fin consists of 13 to 14 rays.

The paired pectoral fins are not visible in specimens 2 and 4 (Figs. 22B, D), but are well preserved in specimen 1 (Fig. 22A) which shows eight small lepidotrichia. The pectoral fin of specimen 3 (Fig. 22C) is preserved only as impression.

Division **Teleostei** Müller, 1845
Order **Pholidophoriformes** Berg, 1937
Family **Pholidophoridae** Woodward, 1890
Genus **Pholidophorus** Agassiz, 1832
Pholidophorus latiusculus Agassiz, 1832
Figure 16C, D

1832 *Pholidophorus latiusculus* – Agassiz: 145.
1905 *Pholidophorus latiusculus* – Gorjanović-Kramberger: 221, Figure 19, Pl. XX Figure 9.
1966 *Pholidophorus latiusculus* – Nybelin: 368, Figures 3, 4, Pl. 4, Pl. 5, Pl. 15 Figures 1, 2, 6, 7.
2013 *Pholidophorus latiusculus* – Arratia: 15, Figures 1, 4–6.

Locus typicus: Seefeld (Tyrol, Austria)

Stratum typicum: „bituminous shales“ of the Norian, Upper Triassic.

Neotype: Collection Dr. Alexander Braun, now in the Museum of Natural History in Karlsruhe, Germany (fide Agassiz, 1832: 145, Nr.1).

Remarks: Agassiz (1832) erected the genus *Pholidophorus* in order to include two species from the Seefeld Member of the type-locality, *P. latiusculus* and *P. pusillus*. The most important features of the original diagnosis given by Agassiz (1832) are: 1) a small-sized body and herring-like shape, 2) large rhomboidal scales, 3) caudal fin with almost equal lobes (whereas scales reach onto the upper lobe), 4) a very small anal fin as well as 5) the dorsal fin situated opposite to the pelvic fins. However, the original material is lost and Agassiz (1832) has not defined a holotype for this species. Nybelin (1966) selected one specimen pictured in Kner (1866) and designated it as neotype of *P. latiusculus* (Innsb. F.123). This specimen is almost complete, but poorly preserved and torn in part and counterpart. Furthermore, it was associated with two labels

which identify it contradictory both as *P. latiusculus* and *P. pusillus* (Agassiz, 1832). Thus, the definition of even this neotype-specimen seems to be disputable, as there is no clearly defined holotype of *P. pusillus*. Even more, as, following the recent monograph of Arratia (2013) about pholidophorids, several specimens originally assigned to the latter species can be reassigned definitely to *P. latiusculus*. Therefore, we act on the assumption that all our (yet restored) pholidophorid specimens should be assigned exclusively to *P. latiusculus*.

Material: 30 well-preserved specimens as well as approximately 100 moderately preserved specimens from bed 6 (fish layer 2).

Description: All specimens of *P. latiusculus* are small-sized with an average body S.L. of ca. 60 mm and show an elongate body with maximum depth in the predorsal region. The pectoral fins are situated directly behind the skull; the small and un conspicuous pelvic fins lie directly opposite to the dorsal fin, the small anal fins oppose the posterior base of the dorsal fin.

As all our specimens of *P. latiusculus* are preserved on plate and counterplate, most of the small-sized skull elements such as the infraorbitals and the suborbitals are not clearly visible. However, the fused roof bones of the skull (compare to Arratia, 2013) build a rather robust, flat and even unit without visible sutures and are usually preserved, as are the triangular opercle, and the bones of the upper and the lower jaw. Especially the dentary with its anterodorsally bent upper margin is often well-preserved. In all our specimens we cannot see any dentition. This might be due to the inadequate preservation, but it appears likely that *Ph. latiusculus* was toothless (compare to Arratia, 2013; however, note the feeble maxillary dentition reported for this species by Nybelin, 1966).

Little can be said about the paired fins. The specimen in Figure 16C shows about six or seven rays in the pelvic fin and 18 to 19 lepidotrichia in the pectoral fin. The hemi-heterocercal, deeply forked caudal fin of the specimen in Figure 16D shows 22 rays.

The fish bodies are covered by ganoid scales of different size and shape as it was already stated in Schultze (1966). Most scales are nearly rhombic to rectangular and have no ornamentation. Towards the tail, the size of scales decreases gradually.

Class **Osteichthyes** Huxley, 1880
Subclass **Sarcopterygii** Romer, 1955
Infraclass **Actinistia** Cope, 1871
Order **Coelacanthiformes** Huxley, 1861
Coelacanth gen. et sp. indet.
Figure 24A

Material: One single scale was found accidentally during the end of our excavation campaign while levelling the site in spring 2014.

Description: The relatively large, circular scale has a maximum length of 32 mm and a maximum width of 31 mm. A part of the scale, probably corresponding to the

anterior area overlapped by preceding scales, is missing (left side in Fig. 24A). The preserved posterior area shows some dozens of slender, oval-shaped hollow ridges which are oriented more the less parallel or arranged at slight angles to each other. In the anterior region, the ridges merge to far over 100 very fine, slightly radial orientated striae. As remains of Upper Triassic coelacanths in the Northern Calcareous Alps so far were unknown and have been described as extremely rare from some Upper Triassic sites in the Southern Alps (Tintori 1991 – however, without presenting appropriate figures) as well as the Middle Triassic of Monte San Giorgio (Rieber 1980), a tentative identification may be done by comparing our scale to one pictured in figure 6 of Wen et al. (2013). The authors describe the scale belonging to the newly erected species *Luoping-coelacanthus eurylacrimalis*, however, without providing an adequate measure. From the scale bar provided in Wen et al. (2013, their figure 5), the specimen possessed scales measuring ca. 5 mm in overall length. Assuming that our scale belongs to a related, not yet described species with similar anatomic proportions, the overall length of the entire coelacanthid fish should exceed 1,20 m.

Fish coprolites

Figure 24C

Material: About a dozen specimens from the beds 2, 3, 7 and 8.

Description: Throughout the lower part of the Seefeld Member, coprolites as fossilized excrements are rare trace fossils. As most of them measure 10 to 55 mm in total length, 2 to 15 mm in total width and contain small filaments (presumably mollusc shells) as well as – as shown in Figure 24C – remnants of small fishes (scales, bones and fragmented lepidotrichia of paired and unpaired fins), we assume that the coprolites derive from large-sized durophagous *Paralepidotus* on the one hand and from the predatory *Saurichthys* on the other hand. Some pieces show a slender, oval shape, some irregular constrictions, but most of them are associated with a mm- to cm-sized halo of carbonates as a sign of the modified micro milieu (enhanced pH value).

Class **Malaostraca** Müller, 1845
Order **Decapoda** Latreille, 1802
Family **Clytiopsidae** Woodward, 1890
Genus **Clytiella** Glaessner, 1931
Clytiella cf. *spinifera* Glaessner, 1931
Figure 24D

1931 *Clytiella spinifera* – Glaessner: Pl. XV, Figure 2, Pl. XVII

Locus typicus: Polzberg near Lunz (Lower Austria, Austria).

Stratum typicum: Reingraben Shales (Lower Lunz Formation, Upper Carnian).

Remarks: *Clytiella spinifera* was first described by Glaessner (1931) from the middle Carnian Polzberg Section

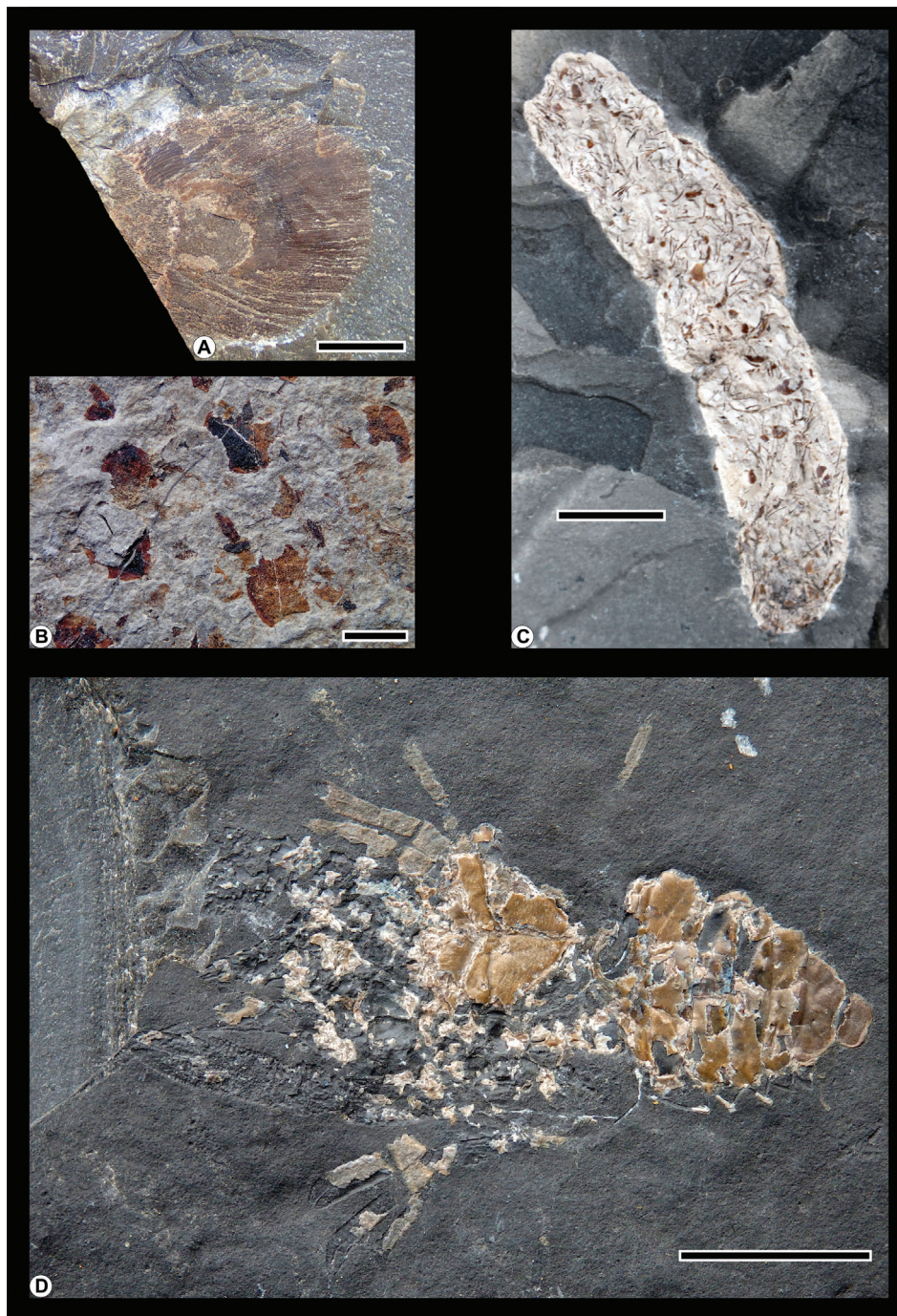


Figure 24: A) Single scale of a large-sized, unknown Coelacanth; B) Unspecified plant chaffs; C) fish coprolite; D) *Clytiella cf. Spinifera*

(Lower Austria). Following Karasawa et al. (2013), the family Clytiopsidae has a stratigraphic range from the Permian to the Upper Triassic (Carnian). We assign the lobster-like crustacean from the Wiestal-site to *Clytiella spinifera* – given that the excavated succession can be dated definitely within the middle Norian, our specimen extends the stratigraphic range of this family from Permian to Norian.

Material: One single specimen was found in the excavated material in context of a “family excursion” during end of excavation and after levelling the digging area (leg. Eva Rossmann, Salzburg, now stored in CGW). Despite several attentive searches, the counterplate remained

undiscovered. Thus, parts of the cephalothorax, the chelipods and some of the walking legs as well as most of the pleopods are preserved as an impression without any fossil substance.

Description: The chitinous carapace is recrystallized into honey-coloured microcrystalline calcite. The best-preserved part of the specimen is the abdomen, showing six smooth, relatively slender segments as well as the left row of the small pleopods, which are preserved partly as imprint. The rounded and rectangular telson is small and inconspicuously stepped. The transition between abdomen and cephalothorax is completely torn apart and

unreconstructable. The posterior part of the cephalothorax shows the median line as well as the both cervical lines in the front and in the back. The preserved carapace is ornamented with a fine crenulation. Whereas the posterior margin of the cephalothorax is partly preserved with a sharp and distinct edge and bordered by a shallow furrow, the anterior rim is torn apart – the rostrum, the eyes and the antennae are completely absent in the imprint. The pereopods show a large carpus and propodus, the first clippers are as long and thick as the pereopod, the surface is ornamented as the carapace. The second clipper is not preserved. The third to fifth period is partly preserved with fossiliferous substance showing a rather small and short clipper above relatively long propodi.

8. Discussion

Besides anatomic details supplementing our knowledge of Triassic actinopterygian fishes, results of the excavation campaign allow to draw several conclusions on the ecology of the fish fauna (Tab. 3), their estimated, relative abundance (Fig. 25) and the palaeoenvironmental conditions in the marine Triassic basins of the Northern Calcareous Alps. Main implications are discussed in the following.

A) Trophic specializations of the Wiestal actinopterygian fishes:

Morphological changes during the ontogeny of *Paralepidotus ornatus* are so striking that they pushed Gorjanović-Kramberger (1905), as well as some of his predecessors and successors, to describe a handful of 'species' attributed to the genera *Colobodius* and *Heterolepidotus*. However, Tintori (1996) reassigned the species listed by Gorjanović-Kramberger (1905) to one single species and referred the differences in body outline, dentition, scale ornamentation as well as the shape of the paired and unpaired fins to ontogenetic stages of *Paralepidotus ornatus*. These morphological transformations should correlate with changes in feeding behaviour and

lifestyle: while the more fusiform, smooth-scaled juvenile *Paralepidotus* are supposed to have lived in schools in open waters and used their more delicate, pointed teeth to feed on crustaceans (Tintori, 1996), the adult form is reconstructed as a slow-swimming but well maneuverable fish, whose crushing dentition was suitable for feeding on large byssate molluscs and echinoderms (Tintori and Olivetti, 1987; Tintori, 1996; Lombardo and Tintori, 2005). Indirect evidence for vast mollusc banks surrounding the deeper lagoonal depressions of the Dolomia Principale of the Bergamasco Prealps ("southern alpine" Hauptdolomit), but hardly preservable due to dolomitization, has been presented by Jadoul (1985) and Tintori (1996), who reported scattered valves of *Modiolus*, *Isognomon* and *Pteria* and bivalve detritus interpreted as predation remains and turbiditic deposits. Tintori and Olivetti (1987) concluded that large *Paralepidotus* moved slowly over the ground, ripping off the large bivalves and crushing their shells, which then were regurgitated. This feeding habit of adult *Paralepidotus* was facilitated by the stub, knob-like teeth, the elongate dorsal fin and the long, fanned pectoral fins allowing precise maneuvering (see Tintori, 1996) as well as by the thick, ornamented scales, enhancing the stability in the water current (see Webb et al., 1992). The rareness of large *Paralepidotus* in the fossil assemblage and its usually isolated occurrence gives more strength to the idea that its preferred habitat was rather remote from the place of burial, so that only some individuals were washed into the anoxic lagoon.

In contrast, the small juvenile and maybe also the sub-adult, medium-sized *Paralepidotus* lived as predatory swarm fishes in open waters. Arguments supporting this hypothesized lifestyle are the slender, fusiform body shape, the relatively small triangular-shaped dorsal fin, smooth scales, the slender pectoral fins and, at last, the dentition. The unornamented squamation in combination with the slender body shape and the small, flat dorsal fin minimized flow resistance. In addition, some fossils make us believe that the long and thin rays of the dorsal

Taxon	Dentition	Body length	Abundance	Trophic niche
<i>Saurichthys</i>	alternation of large and small conical teeth	>110 cm	rare	large pelagic predator
<i>Legnonotus</i>	small, very thin teeth	<10 cm	moderate	soft-bodied invertebrate feeder
<i>Semiolepis</i>	marginal teeth conical, partly bent backwards; coronoid teeth with stout, apically rounded	>25 cm	rare	mid-sized durophagous feeder
<i>Paralepidotus</i> (juvenile)	small, slender and high-crowned teeth with an apical tubercle	<25 cm	very abundant	predator on swimming crustaceans
<i>Paralepidotus</i> (adult)	crushing	>25 cm	abundant	large durophagous feeder
<i>Dandya</i>	slender, pointed prehensile teeth and crushing vomerine and palatine teeth	<5 cm	rare	invertebrate feeder
<i>Eomesodon</i>	crushing	<4 cm	rather rare	small durophagous feeder
<i>Pholidophorus</i>	weak or absent	<6 cm	moderate	microphagous
<i>Coelacanth</i>	few fangs on the palate	>100 cm	very rare	large bottom-dwelling predator

Table 3: Trophic specialization of the fish species found at the Wiestal site.

fin were highly flexible and could be actively collapsed when necessary (e.g. for high-velocity swimming; see Lauder, 2015) to form only a flat dorsal ridge. The slender pectoral fin was probably also flexible enough to be folded closely to the anterior body. The dentition made up of slender teeth with a central tubercle allowed the capture of small mobile prey and was probably strong enough to crush the exoskeleton of small crustaceans.

The assumption that small *Paralepidotus* have lived in large swarms is substantiated by the fact that many of them have been found in fossilized fish accumulations at the Wiestal site, e.g., in fish-layers 3 and 4, documenting a mass-mortality amongst small-sized fishes of different species. *Legnonotus* and *Pholidophorus*, as well, may have lived in schools (fish layer 2). *Legnonotus* with its fusiform shape, its (most probably) flexible, fanned dorsal fin and its pen-like, not very stout teeth may have chased for small swimming, thin-shelled crustaceans and smaller juvenile fishes. The small fusiform and most probably toothless *Pholidophorus* may have lived in large swarms, probably similar to recent herrings, feeding on marine phytoplankton that prospered during Late Triassic times (S. Richoz, Lund, pers. comm.). The small high-bodied fishes *Eomesodon* and *Dandya* can be reconstructed as invertebrate feeders, with *Eomesodon* being better adapted to durophagy. *Semiolepis* presumably was a mid-sized durophagous feeder, similar in habitus compared to the adult *Paralepidotus* (Lombardo and Tintori, 2008), but somewhat smaller. The fast-start predator *Saurichthys*

and the presumably slow-swimming, bottom-dwelling coelacanth (see Lombardo and Tintori, 2005; Kogan et al., 2015) occupied the highest trophic level.

B) The sedimentary history of the Wiestal site

The fine-grained, regularly laminated deposits at the Wiestal site point to quiet, protected and stagnant lagoonal waters that were responsible for the remarkable and excellent fossil preservation. The undisturbed mm-scale lamination of the dolostones implies the complete absence of any benthonic, bottom-dwelling fauna. The perfect and nearly exclusive articulation of any fossil substance as well as the high TOC because of incomplete necrotic decay of organic matter, speaks in favour of a strictly anoxic water body that was developed in the Wiestal (and Seefeld) basins at greater water depths below the wave base.

Apart from the understanding of mechanisms leading to anoxic water stratification (euxinic model) in modern environments (Demaison and Moore, 1980), the applicability of these mechanisms to restricted Late Triassic lagoonal basins is substantially questionable (e.g., Tintori, 1992). Part of the analogy problem is that, while modern basins generating anoxia are surrounded by land, the deeper water areas of the Alpine Late Triassic have been surrounded by carbonate platforms. This fact, however, ensured a constant supply of marine water of normal salinity and oxygenation, which would be subject to evaporation under the Norian hot semi-arid climatic conditions (e.g. Preto et al., 2010 and references therein).

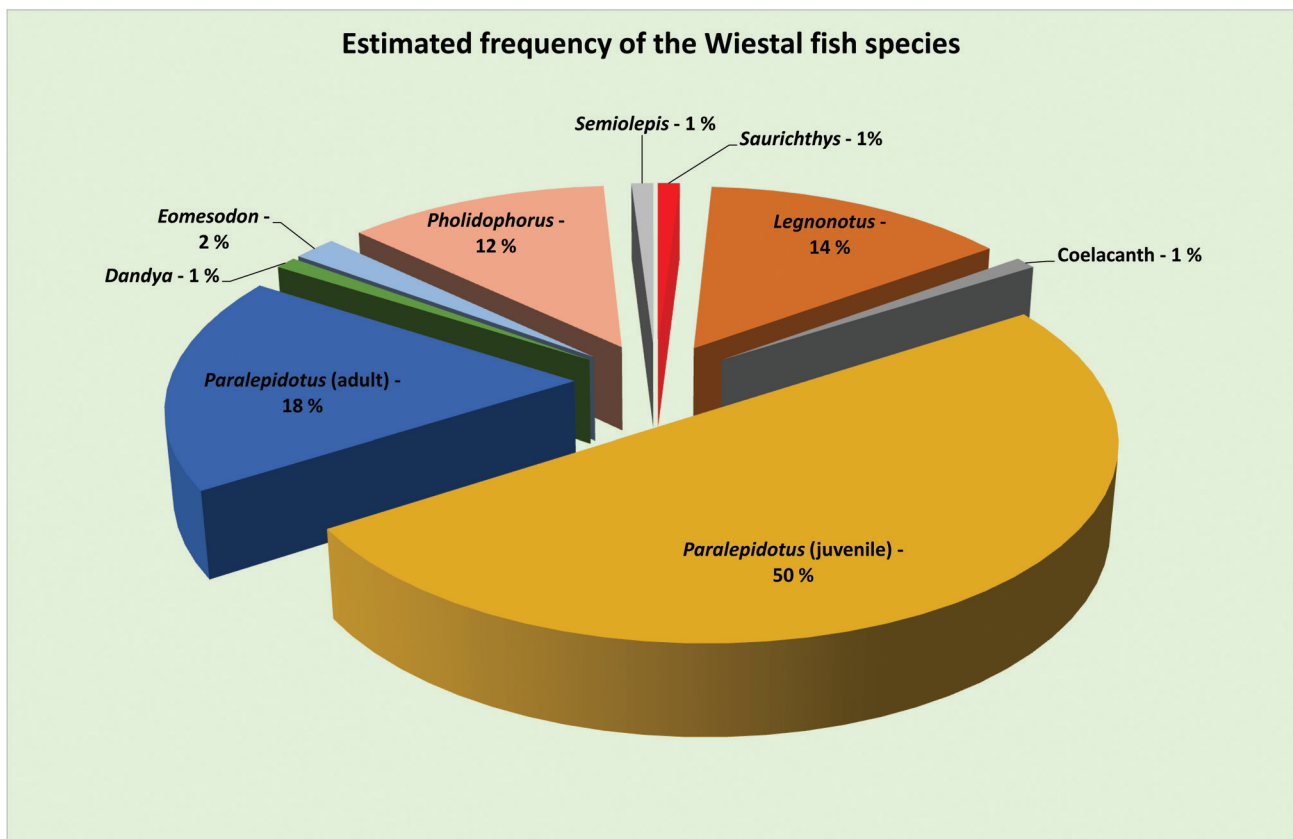


Figure 25: Abundance of the actinopterygian fish remains found at the Wiestal site.

The heavier hypersaline waters would then sink to local depressions such as the Wiestal basin, creating regions of permanent water stratification with a persistent chemocline. A similar pattern has been described from the Late Jurassic Solnhofen archipelago (Arratia et al., 2015), from the Middle Triassic fossil concentrations of Monte San Giorgio (Rieber, 2000) and from Italian alpine Triassic localities (Tintori, 1992). This scenario is favoured, too, by Bechtel et al. (2007) for the Wiestal area, who refer to organic geochemistry data as evidenced by molecular indicators. Indeed, habitation, climate and sedimentary history of the Upper Triassic successions exposed at the Wiestal site, should have been comparable to Monte San Giorgio, even though the bottom-near water body was dysoxic with rare evidence of bioturbation (Tintori 1992).

The large-scale intertidal to subtidal flats where the Hauptdolomit formed provided quiet marine conditions. Most probably, the shallow-marine area was drained onshore by large tide channels and punctuated with some flat but isolated, tectonically induced basins and depressions. Already Tintori (1992) supposed that the saline, heavy and dense surface water that was produced in the shallowest littoral regions was sloshed down through deep tidal channels across the Hauptdolomit-lagoon and got enriched within the isolated basins. As dolomite and no gypsum precipitated, the salinity in those depressions should not have exceeded 115 per thousand (Barthel et al., 1990). The normally oxygenated, mesohaline surface water comprised a rich nektonic fauna with high bioproductivity rates (Bechtel et al., 2007). Organic material both of the macrofauna and upcoming zooplankton (e.g., radiolarians) trickled down and got enriched at the basin depths, depleting the oxygen and maturing to hydrogen sulphides (H_2S) (Bechtel et al., 2007). This anoxic environment excluded scavengers as well as any benthonic life, slowed down and, finally, stopped the microbial decay of the carcasses of the macrofauna sinking to the bottom of the basins. The hydrogen sulphide can have partly reacted with iron to produce iron sulphides (Pyrite), which are very stable in anoxic water (Goldman and Horne, 1983). The other part of H_2S -gases was trapped by the stable halocline within the basin depths. This effect has been strengthened by the limited renewal of water within the lagoon.

C) A short explanatory model of the Wiestal fossil-concentration

To understand the processes that led to the fossil concentrations at the Wiestal site, it is necessary to have a closer look on the fossil taphonomy and its palaeoecologic implications.

Fishes with their great number of skeletal elements are very sensitive and vulnerable to decay (Schäfer, 1972). Thus, the mode of decay and embedding – in other words – the biostratinomy and taphonomy of fishes, can be an effective tool to reconstruct depositional conditions of their habitat or place of burial (Tintori, 1992). Normally, most fish carcasses float after death for a while at

or near the water surface, often under loss of parts of the skeleton. However, Triassic ganoid fishes are often found articulated, owing to their heavy, tightly connected exoskeleton (Tintori, 1992): there is not enough necrotic gas and/or gas in the air bladder allowing the carcasses to rise towards the water surface. Accordingly, we found only complete and articulate skeletons of medium-sized to large, heavy fishes such as adult *Paralepidotus*, *Semiolepis* and *Saurichthys* (standard length > 30 cm). Even almost all of our small-sized swarm-species (*Pholidophorus*, *Legnonotus*, *Dandya* and *Eomesodon*) show an anatomically articulate preservation. Only one specimen of *Legnonotus krambergeri* was found as a stray find in layer 3, with a disarticulated skull and a disjointed postcranial skeleton. Thus, fish taphonomy at the Wiestal site is homogenous and, in case of the spectacular fossil concentrations in distinct horizons, implies following frame conditions:

- 1) Death of the organisms had to happen simultaneously and rather quickly.
- 2) There was no or only minimal floating of dead fish bodies in the water column and rare scavengers – all carcasses must have quickly reached the bottom of the small basins.
- 3) The skeletons were not dismembered during the whole decay till embedding.

Due to the anoxic bottom water, there were no benthic organisms that could have caused disarticulation by scavenging. The complete absence of aerobic protozoans and prokaryotes as well as the assumed rareness of anaerobic bacteria allowed soft part preservation as observed on large-sized (*Saurichthys*, Figs. 13, 14) and even small fishes (blackish hue in the eyehole of *Eomesodon*, see Figs. 21 and 22).

But what mechanism could have led repeatedly to quick death of single fishes or even complete swarms? In four of our five fish layers (layer 1, 3, 4 and 5) the “fish kills” affected both small- and large-sized fishes: small swarm-fishes (*Legnonotus*, *Pholidophorus* as well as juvenile *Paralepidotus*), small durophagous feeders (*Eomesodon*) and large durophagous feeders (adult *Paralepidotus*) as well as large predators (*Saurichthys*). In case of the fish-layer 2, the event apparently affected only small-sized swarm-fishes that lived in open waters. The presence of large-sized *Paralepidotus* shows that “fish kill” events reached even fishes whose preferred habitat was at or near the basin margins where byssate molluscs lived. In other words, the fish layers preserved a representative average of ganoid fish fauna that both thrived in the open waters of the Hauptdolomit lagoon and lived in proximate habitats around the basins. The flat depressions themselves were uninhabited due to the anaerobic environment.

To summarize these observations, we need a short-pulsed, rapid mechanism that poisoned the pelagic and near-shore shallow waters in such dimensions that even fast-swimming predators were not able to escape or swim away. Such “fish kill”-events are usually induced by algal

blooms or by storms lifting masses of highly saline and anoxic bottom water. During the Triassic, most continents were integrated in the supercontinent Pangaea, surrounded by the Panthalassa Ocean. Pangaea straddled the equator, and a huge gulf (Tethys) was open on the eastern side of the supercontinent. This extended landmass led to extreme climates in the Tethys region, characterized by enhanced monsoonal atmospheric circulation (“megamonsoon” of Kutzbach and Gallimore, 1989; Dubiel et al., 1991; Loope et al., 2001). During these extreme climatic conditions,

severe tropical storms ravaged recurrently the Pangaeian coastlines of the austroalpine domain and resulted in the mixture of surface and bottom water near the halocline. This produced a short-pulsed intoxication of the upper water body and affected both single large fishes and fish swarms that sojourned in greater water depths than normal to elude the heavy sea. The fishes died immediately when swimming through the slurry mixed up of clay particles and poisonous substances due to loss of orientation, abrupt absence of oxygen and agglutination of their gills (Fig. 26).

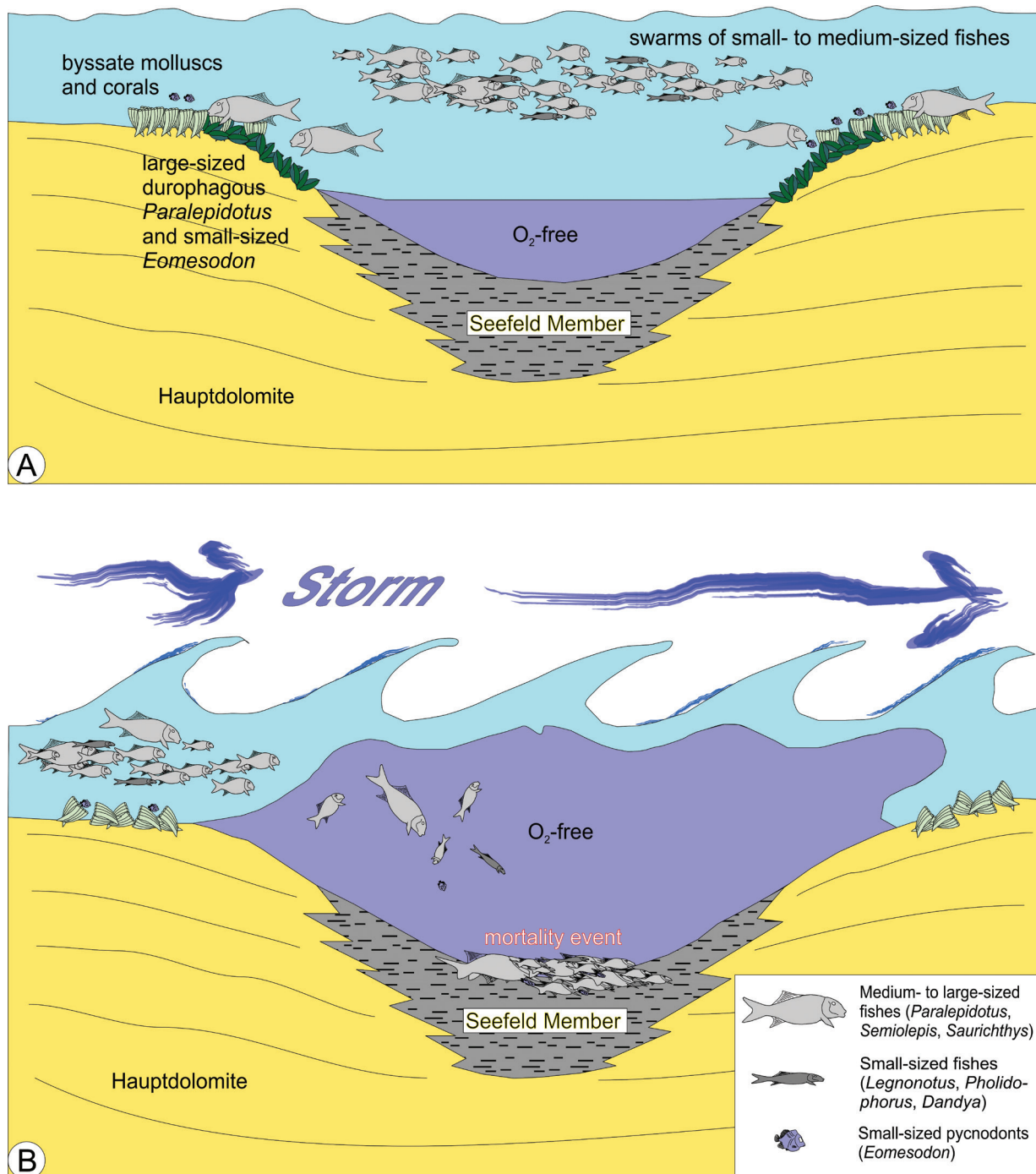


Figure 26: Schematic sketch showing the presumed genesis of the Wiestal fossil deposit. Picture A demonstrates the normal condition with normal oxygenated surface water and an oxygen-free, highly saline stratified water body that is replenished in the flat Seefeld depressions. Periodically occurring tropical storms stir up the complete water body leading to an upwelling of toxic bottom water that, in turn, causes sudden death of both single fishes and complete fish swarms.

As the tropical cyclones most probably were accompanied by severe rainstorms, they should have caused perturbations to the shallow-marine area and the adjacent hinterland and/or islands. Therefore, we normally should have found detritus of byssate molluscs that lived near the basin margins, other benthonic organisms such as gastropods, crinoids and crustaceans, other nektonic organisms such as ammonoids or nautiloids as well as land plants during our excavation. In fact, the fish layers contained only disintegrated plants as parts of single leaves (Figs. 6, 11), plant chaff (Fig. 23B) and occasionally occurring driftwood (gagate, see Fig. 7) and only one crustacean (*Clytiella* cf. *spinifera*, Fig. 23D). Furthermore, we have no signs of real tempestite layers including larger intra- and extraclasts. One possible explanation may be that the fish-kill-events may have been initiated by severe squalls that preceded cyclonic rainstorms. The winds lower the storm wave base into the anoxic basins, stir up the toxic water body and cause the fish extinction events which were not coercively accompanied by tempestite marks.

During and after the storm, the fish carcasses sank to the anoxic bottom of the Wiestal lagoon. Isoorientation of some specimens indicates the presence of bottom currents in the first stages of burial; size-dependent sorting of the fishes can be related to interactions between the currents, fish bodies and the soft sediment. Finally, the stirred sea precipitated fine clayey and calcareous particles – sometimes mixed with fine plant chaff – into the basins that caused a quick covering of the carcasses, before the previous water stratification re-established, preventing decay of the fish bodies.

The deposition of the Seefeld Member at the Wiestal site certainly lasted for several ten thousands of years and witnessed numerous storms and cyclones during that time. As we found “only” five fossil horizons, it is clear that a “normal” storm could not have resulted automatically in a “fish kill” event. In other words, the Wiestal basin with its anoxic bottom water must have been rather deep (several tens of meters). Only a very severe storm (“mega-hurricane”) was able to depress the storm wave base to a level that reached the highly toxic bottom water and released the processes that are highlighted above.

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