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Source: Palaeodiversity, 14(1) : 15-113

Published By: Stuttgart State Museum of Natural History

URL: <https://doi.org/10.18476/pale.v14.a3>

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The Middle Jurassic Opalinuston Formation (Aalenian, Opalinum Zone) at its type locality near Bad Boll and adjacent outcrops (Swabian Alb, SW Germany)

VOLKER DIETZE, STEFAN GRÄBENSTEIN, MATTHIAS FRANZ, GÜNTER SCHWEIGERT & ANDREAS WETZEL

Abstract

The lithostratigraphy and ammonite biostratigraphy of the Middle Jurassic Opalinuston Formation in the Teufelsloch gorge at Bad Boll (middle Swabian Alb), which is the type locality of this formation and that of its lower member, the Teufelsloch Member, is described. The term Comptum Subzone, formerly well established in SW Germany, is replaced by the Bifidatum Subzone. Additionally, the regional term Comptumbank bed is replaced by Wilflingen-Bank and the local term Costosumbank bed is replaced by Bifidatumbank. Four ammonite biohorizons (*opalinum*, *dilucidum*, *opaliniforme* and *hansrieberi* biohorizons) of the Opalinum Subzone and three ammonite biohorizons (*bifidatum/rieberi*, *uncinatum* and *evolutum* biohorizons) of the Bifidatum Subzone (formerly “Comptum Subzone”) are described from the type locality. The *crassicosatum* biohorizon of the Bifidatum Subzone is introduced in the western Swabian Alb. The biostratigraphical boundary between the Opalinum and Murchisonae zones (Lower/Upper Aalenian) is located at the base of the Achdorf Formation. The succession is compared and correlated with other localities in Germany and Europe. The species of the ammonite genus *Leioceras* are described using a chronospecies concept. Lectotypes are designated for *Leioceras partitum* (BUCKMAN, 1899) and *Leioceras uncinatum* (BUCKMAN, 1899). We briefly report on the macrofauna of the Opalinuston Formation. In addition, we provide important petrographical, sedimentological and geochemical information for the understanding of the depositional conditions for some selected layers.

Key words: Opalinuston Formation, lithostratigraphy, sedimentology, petrography, biostratigraphy, ammonite fauna, correlation, *Leioceras*.

1. Introduction

The oldest illustration of an ammonite (*Pleurolytoceras*) from the Middle Jurassic of Bad Boll dates back to the end of the 16th Century (BAUHNUS 1598, 1602; HEGELE 1995: 93, re-illustration on top). ZIETEN (1830) added a *Leioceras* (*Ammonites opalinus*) from the Teufelsloch gorge. Under the heading “Opalinuston”; QUENSTEDT (1843) cited the steep slopes of the Teufelsloch gorge at Boll, where a well-known, rich assemblage of fossils occurs in black claystones with *Ammonites opalinus*. This citation made the Teufelsloch gorge the type locality of the present-day Middle Jurassic Opalinuston Formation and recently it was designated as the type locality of the Teufelsloch Member (FRANZ & NITSCH 2009). Subsequently, SCHMIDT (1846) described ammonites and bivalves from the “Opalinuston” of the Teufelsloch gorge. QUENSTEDT (1846–1849, pl. 7, fig. 10) illustrated a specimen of *Ammonites opalinus* from the “Oberregion des Braunen Jura α” (upper part of the Opalinuston Formation) of this locality. Subsequently, QUENSTEDT (1857) considered the Teufelsloch gorge and Zillhausen in the western part of the Swabian Alb as being the best localities for the study of this formation. In his classical monograph on ammonites of the Swabian Jurassic (Die Ammoniten des Schwäbischen Jura. 2. Der Braune Jura), QUENSTEDT (1886) described numer-

ous ammonites from the Teufelsloch gorge, Bad Boll and nearby Gammelshausen. QUENSTEDT’s student ALBERT OPPEL, the founder of the zonal concept in biostratigraphy, cited the vicinity of Boll and the Teufelsloch gorge near Boll as typical of his ‘Zone der *Trigonia navis*’ (OPPEL 1856). Brief descriptions of the section exposed in the Teufelsloch gorge have been provided by ENGEL (1883), BOTZENHARDT (1936), SÖLL (1954), GOTTLIEB (1955), WEBER (1964), and ANDALIB (1970). The most detailed descriptions of the section and its palaeontology are by GROPPER (1925) and KOBLE (1967, 1972). HEGELE (1992, 1995, 2009) described and illustrated the section and numerous fossils from the Opalinuston Formation in the Teufelsloch gorge and from the nearby disused clay pit Mohring at Heiningen. OHMERT (1993) produced the first biostratigraphical subdivision of the Opalinuston Formation in SW Germany below the level of subzones. He studied sections of the Opalinuston Formation exposed in several creeks in the close vicinity of Bad Boll (Mühlbach, Riesbach, Teufelsklingsbach, Pliensbach, Rotensteigbach) and differentiated three ammonite horizons within the Opalinum Subzone (*opaliniforme*, *partitum* and *lineatum-costosum* horizons). Here we regard these ‘ammonite horizons’ (sensu CALLOMON 1995) as ‘biohorizons’, each comprising a bed or a set of beds with an indistinguishable ammonite fauna.

At the occasion of the construction of the new motorway A8, DIETL (1988: 19) measured the section of the Opalinuston Formation along the Aichelberg slope. His section differs significantly from the section of FRANZ & NITSCH (2009) both in the identification of beds and in their thicknesses. Compared with our observations, the section of FRANZ & NITSCH (2009) is correct.

The aims of this work are to describe the lithostratigraphy, biostratigraphy and ammonite fauna of the Opalinuston Formation at its type locality. Additionally some interesting petrographical and sedimentological aspects are illuminated.

Abbreviations: GPIT = Palaeontological collection of Eberhard-Karls-Universität Tübingen, Germany; LGRB = Landesamt für Geologie, Rohstoffe und Bergbau im Regierungspräsidium Freiburg i. Br., Germany; NMBE = Naturhistorisches Museum Bern, Switzerland; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany; HT = holotype; LT = lectotype; [M] = macroconch; [m] = microconch; OpK = “Opalinusknohle” (concretion containing ammonites).

2. Geological setting and material

2.1. Geological setting

South of Bad Boll-Eckwälden (middle Swabian Alb, Fig. 1), the Teufelsklingsenbach creek is a deep gorge cut into the claystones of the Opalinuston Formation (Braunjura Group), the so-called ‘Teufelsloch’. In this area, the Opalinuston Formation (or ‘Opalinuston’ in older literature) has a thickness of c. 130 metres (OHMERT 1993, and below). The basal few metres of the Opalinuston-Formation crop out in the bed of the Teufelsklingsenbach creek in the village of Bad Boll-Eckwälden. The lowest few metres of the Opalinuston Formation and the Jurensismergel Formation (Schwarzjura Group) below are very poorly exposed in the Teufelsklingsenbach creek and cannot be examined anymore. Therefore, in this study, we included exposures in two tributaries of the Pliensbach creek located nearby and the disused clay pit in Heiningen

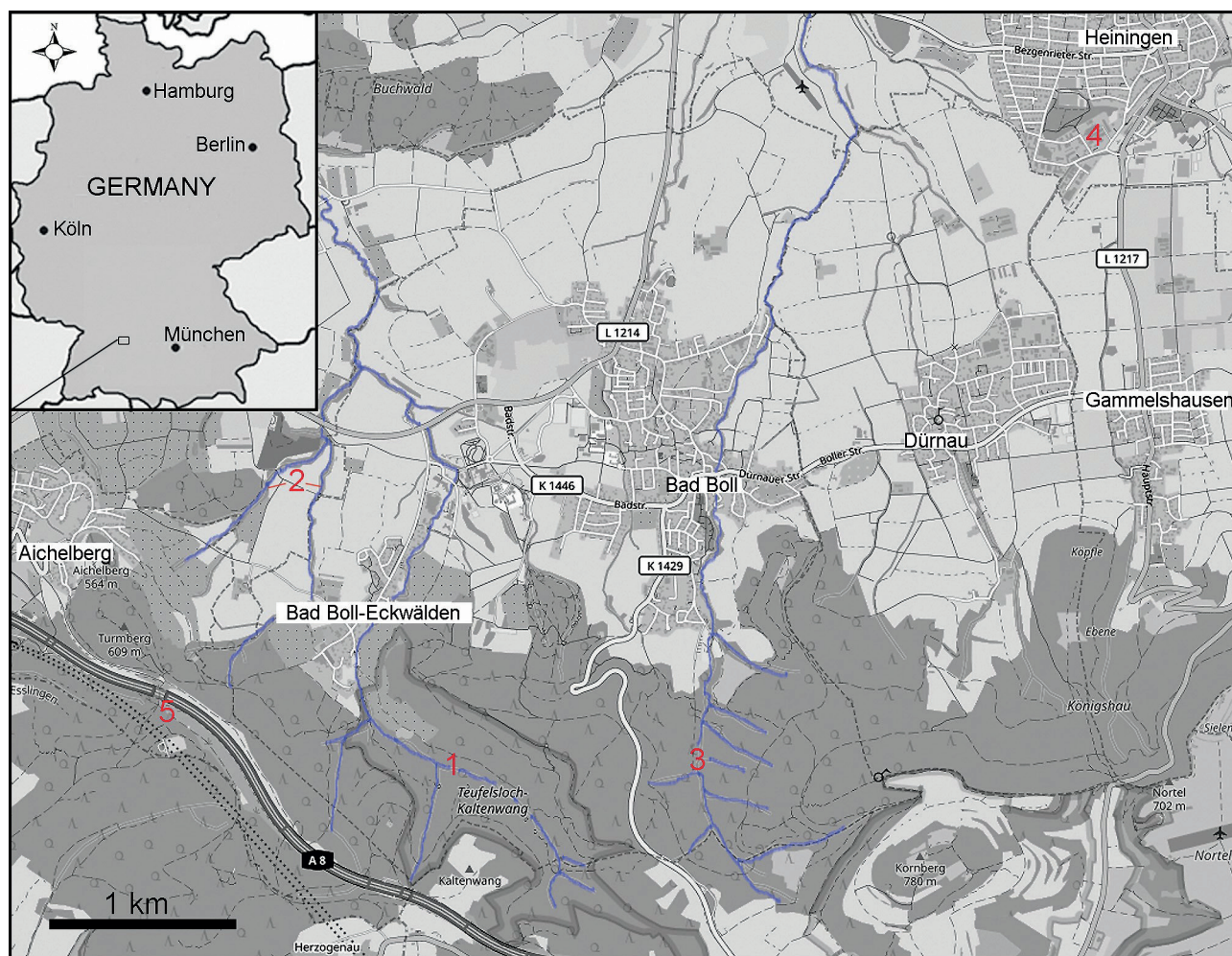


Fig. 1. Location of the outcrops in the Teufelsklingsenbach (1), Pliensbach (2) and Riesbach (3) creeks at Bad Boll, the former Opalinuston clay pit Mohring in Heiningen (4) and the outcrop “Grünbrücke” at the motorway A8 (5).

(c. 5 km away) in the description of this basal part of the Opalinuston Formation. (Fig. 1). The Teufelsklingenbach creek, which joins the Pliensbach creek slightly north of the road L 1214, together with some of its tributaries, cuts the complete Middle Jurassic succession. Similarly, northeast of the road K 1429 connecting Bad Boll and Gruibingen, the Riesbach creek cuts the Opalinuston Formation (Fig. 1). Since the sections of the Opalinuston Formation are considered nearly identical in the Riesbach and Teufelsklingenbach creeks, we also included some specimens from the Riesbach section. At the ‘Grünbrücke’ (a tunnel-like bridge constructed for wildlife to cross the motorway A 8 at the Aichelberg in a distance of less than 2 km from the section in the Teufelsklingenbach creek and south of the tributaries of the Pliensbach creek), the transition between the Opalinuston and Achdorf formations can be investigated and thus, we added this outcrop to our study (Fig. 1). The base of the Achdorf Formation coincides with the base of the ‘Comptumbank’ (FRANZ & NITSCH 2009). This bed is renamed due to an erroneous interpretation of the name-bearing taxon *Nautilus comptus* REINECKE, 1818 (for details, see p. 28).

2.2. Material

A small number of the illustrated specimens (originally studied by OHMERT 1993) are housed in the collection of the Landesamt für Geologie, Rohstoffe und Bergbau in Freiburg. Specimens from the basal part of the Teufelsklingenbach section (“Torulosum-Knollenlage”) are housed in the collection of the Naturhistorisches Museum Bern (ex collection O. HUG, sampled in 1899). Further specimens studied from the basal part of the Teufelsloch gorge (“Torulosum-Knollenlage”) are housed in the palaeontological collection of Tübingen University. Ammonites from the basal part of the Pliensbach section (“Torulosum-Knollenlage”) come from the collection of G. GASSMANN donated in 2001. The bulk of the newly collected and figured specimens are housed in the collection of the Stuttgart Natural History Museum (SMNS; accession numbers are given in the figure captions).

3. Lithostratigraphy and ammonite faunas

3.1. Opalinuston Formation

The Opalinuston Formation comprises two members, the clayey Teufelsloch Member below and the silty Zillhausen Member above (FRANZ & NITSCH 2009). The base of the formation is defined by the onset of dark claystones above the Jurensismergel Formation and its top coincides with the base of the Comptumbank (now Wilflingen-

Bank) of the Upper Aalenian Achdorf Formation (WENK 1927; FRANZ & NITSCH 2009). In the study area, the Achdorf Formation intergrades with sandstones of the Eisen-sandstein Formation, which becomes predominant in Eastern Swabia and Franconia (FRANZ & NITSCH 2009).

Lithologically, the claystones of the Teufelsloch Member are the product of fully marine subtidal mudstone deposits, with low bottom currents and temporary anoxic environmental conditions. In the Zillhausen Member above, there is a gradual change upwards to arenaceous deposits with intercalated thin subtidal sand bars (Wasserfallschichten, Zopfplatten) and local tempestite layers (belemnite breccia) (FRANZ & NITSCH 2009). The Opalinuston Formation has a total thickness of c. 130 m (OHMERT 1993: fig. 2 [corrected here by -10 m, see below]). This is more than one third of the thickness of the entire Braunjura Group (GEYER & GWINNER 2011). The main reason for the enormous thickness of the Opalinuston Formation is a marked increase in sediment accumulation rate (FRANZ & NITSCH 2009).

The main objective of this work is to focus on the lithostratigraphical subdivision and ammonite biostratigraphy of the Opalinuston Formation (Fig. 2). We therefore only refer to the palaeoenvironmental studies of this formation by WETZEL & ALLIA (1996, 2000, 2003) and WETZEL et al. (2003). The Opalinuston Formation in Southern Germany and adjacent Northern Switzerland accumulated in an epicontinental shallow marine setting. The estimated water depth during the deposition of the Teufelsloch Member was in the range of a few tens of metres and in the overlying Zillhausen Member c. 20–30 m or even less. Argillaceous muddeposited from suspension formed claystones. The sand deposits typical of the Zillhausen Member were formed around storm wave base. The bulk of the sediment input derived from rivers of the Bohemian Massif in the East and the Vindelician High in the Southeast. Over the same time as the high sediment input was taking place subsidence of the basement occurred resulting in the great thickness of the strongly compacted claystones.

Biostratigraphically, the Opalinuston Formation represents only a single ammonite zone (Opalinum Zone, Lower Aalenian), except for some thin basal beds locally still belonging to the Late Toarcian Aalensis Zone. The upper boundary of the Opalinum Zone is located just below the base of the Achdorf Formation.

3.1.1. Teufelsloch Member

The Teufelsloch Member, formally introduced by FRANZ & NITSCH (2009), has not been further subdivided. Here we use traditional terms taken from older literature for some distinguishable beds within this member.

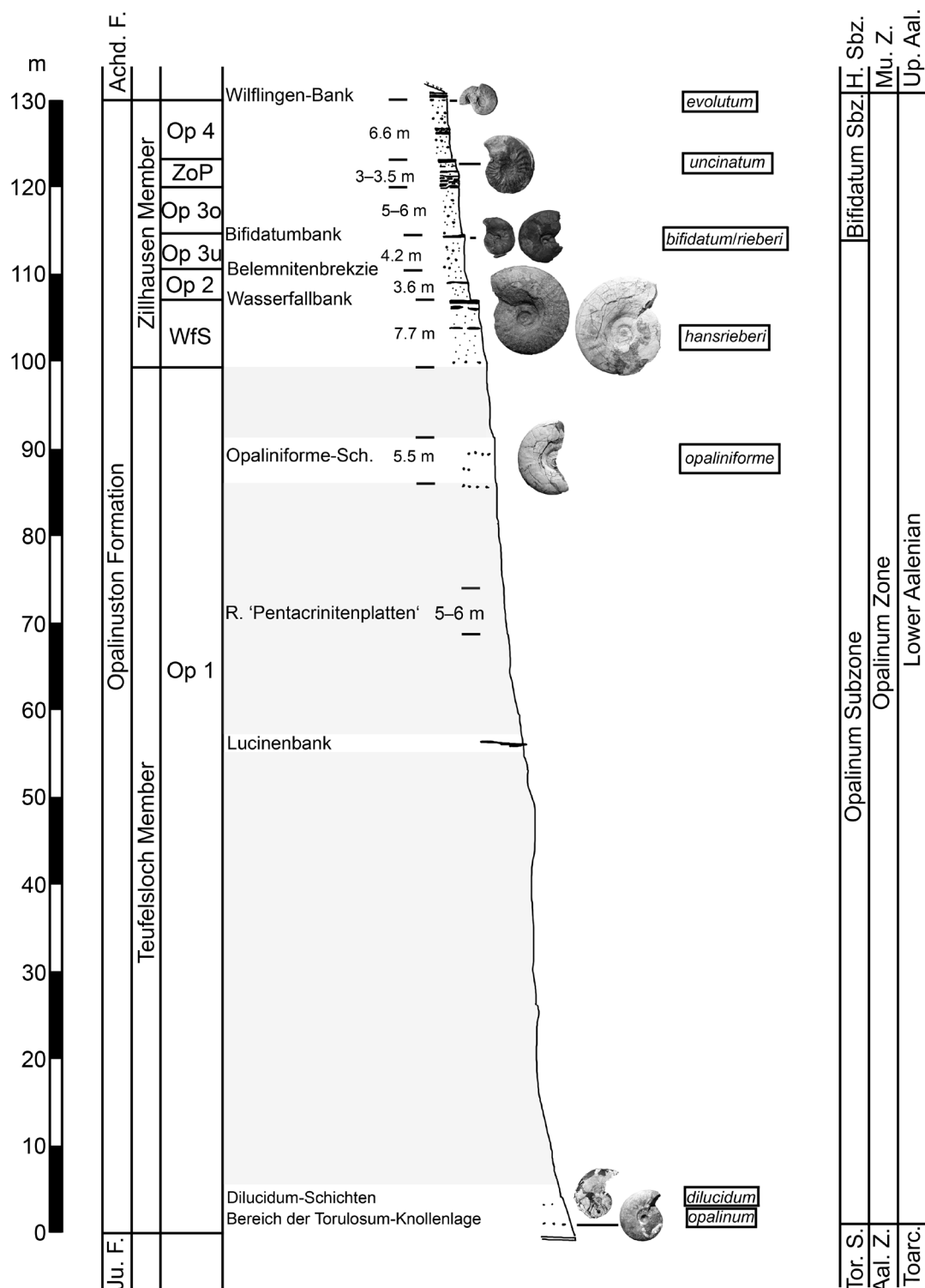


Fig. 2. Combined section of the Opalinuston Formation (Lower Aalenian) in the Teufelsklängenbach creek at Bad Boll-Eckwälden (section above the Dilucidum-Schichten) and in the tributaries of the Pliensbach creek (section up to the Dilucidum-Schichten). The grey parts of the section were not studied in detail due to the outcrop situation or the rarity of ammonites. Ju. F. = Jurensismergel Formation; Op = Opalinuston Formation; L. 'Pentacrinitenplatten' = Level of the 'Pentacrinitenplatten'; Opaliniforme-Sch. = Opaliniforme-Schichten; WfS = Wasserfallschichten; ZoP = Level of the 'Zopfplatten'; Achd. F. = Achdorf Formation; H. Sbz. = Haugi Subzone, Mu. Z. = Murchisonae Zone, Up. Aal. = Upper Aalenian, Tor. S. = Torulosum Subzone, Aal. Z. = Aalensis Zone, Toarc. = Toarcian.

The exact position of the base of the Teufelsloch Member in the Teufelsklingenbach creek is unknown due to poor exposure (GROPPER 1925). Therefore, we included information from the western and eastern tributaries of the nearby Pliensbach creek and from the former clay pit Mohring in Heiningen. GOTTLIEB (1955) described the underlying Jurensismergel Formation (“Lias zeta”) of the Teufelsklingenbach creek.

We focused on parts of the section presently accessible for investigations and which are relatively rich in ammonites and thus, biostratigraphically interpretable. A comparison with previous studies (KOBLE 1967, 1972; OHMERT 1993) revealed that all biostratigraphically relevant parts of the Teufelsloch Member could be restudied. Only the lower part of this member, the claystone unit above the “Dilucidum-Schichten”, contains very rare fossils.

3.1.1.1. Range area of the ‘Torulosum-Knollenlage’ and ‘Dilucidum-Schichten’

A. Teufelsklingenbach creek

GOTTLIEB (1955) briefly described the underlying Jurensismergel Formation (“Lias zeta”) of the Teufelsklingenbach creek. Due to lack of exposure in the Teufelsklingenbach creek no new material from the basal Opalinuston Formation was collected. The ammonites studied are from museum collections. All these specimens were preserved inside limestone concretions or in the body chambers of large lytoceratids.

Ammonites: *L. opalinum* α (Pl. 1, Fig. 11), *L. opalinum* var. *comatum* (Pl. 1, Fig. 4), *L. opalinum* α var. *buckmani* (Pl. 1, Figs. 7, 9, 10, 13), *L. opalinum* α var. *tomum* (Pl. 1, Fig. 14), *L. opalinum* α var. *costulatum* (Pl. 1, Fig. 15), *L. opalinum* α var. *subcostosum* (Pl. 1, Fig. 12), *L. opalinum* α var. *leurum* (Pl. 1, Fig. 8; Pl. 2, Fig. 6), *L. opalinum* α var. *subglabrum* (Pl. 1, Figs. 2, 5, 6), *Pleurolytoceras torulosum* (Pl. 1, Figs. 1, 3), *P. penicillatum*.

B. Tributaries of the Pliensbach creek

The two tributaries of the Pliensbach creek are located west of the village of Bad Boll-Eckwälden (Fig. 1). They meet just before the road L 1214. In the outcrop area of the basal Opalinuston Formation, the gradient of the creeks is so low that the thicknesses of the incompletely exposed section can only be roughly estimated.

In the western tributary of the Pliensbach creek, we recorded the following incomplete section at the base of the Opalinuston Formation:

Transition Jurensismergel Formation / Opalinuston Formation:

- (0.3 m): Brownish marl at the top of the Jurensismergel Formation.
- (~ 1–1.5 m): Within this interval the boundary between the Jurensismergel and Opalinuston formations and the basal-most

part of the Opalinuston Formation with the Torulosum-Knollen is located. These beds are now obscured. The thickness of the beds following up to c. 1.0 m above the “Dilucidum-Schichten” (Opalinuston-Formation) can only be roughly estimated due to the poor exposure, weathering and almost horizontal bedding (after KOBLE 1967, the dip of the beds in the Teufelsklingenbach creek is 2–3° towards the Southeast).

GOTTLIEB (1955: 39) described a 0.08 m thick bed of calcareous marl overlain by 0.97 m steel-grey marl containing fragments of *Cotteswoldia aalensis*. Above, 0.4 m of ochre-coloured marl with *Leioceras opalinum* and *P. torulosum* is overlain by a 0.05 m thick layer with white aragonitic shells, 0.3 m grey-green marl and finally 0.25 m grey-olive marly mudstones full of aragonitic *P. torulosum*, bivalve debris and belemnites. We have doubts regarding the correct determination of *Leioceras opalinum* in the abovementioned marls. They may represent morphologically similar *Pleydellia* spp. of the latest Toarcian. GOTTLIEB (1955) placed the boundary between the Jurensismergel and Opalinuston formations at the base of the 0.25 m thick claystone with *P. torulosum*.

Dilucidum-Schichten:

- (~ 0.7–1.0 m [beds below not exposed]): Strongly weathered claystone with numerous compressed white aragonitic shells of *Leioceras opalinum* β and *Pleurolytoceras dilucidum* (“beer-mat shells” sensu SEILACHER et al. 1976).

- (~ 0.35 m): Claystone with a layer of grey, oval limestone concretions, rarely with fragments of white-shelled *L. opalinum* β and *Pleurolytoceras dilucidum* on their upper surface. Claystone with mass occurrence of compressed white aragonitic shells of *L. opalinum* β and abundant *P. dilucidum*.

- (~ 1.3 m; in the middle there is a small waterfall with a height of c. 0.7 m): mass-occurrence of compressed white-shelled *L. opalinum* β and abundant *P. dilucidum*. Two specimens of *Bredia subinsignis* have been recovered from the claystones at the top of the small waterfall, which yield a mass occurrence of the gastropod *Toarctocera subpunctata*. Nuclei of ammonites are sometimes three-dimensionally preserved. A large limestone concretion from just above the small waterfall has yielded the fish *Dapedium ballei* (MAXWELL & LÓPEZ-ARBARELLO 2018).

Ammonites: *Leioceras opalinum* β (Pl. 3, Figs. 2, 3, 6, 10, 12), *L. opalinum* β var. *buckmani* (Pl. 3, Figs. 4, 5, 7), *L. opalinum* β var. *undatum* (Pl. 3, Figs. 8, 11), *L. opalinum* β var. *subglabrum* (Pl. 3, Fig. 9), *Bredia subinsignis* (Pl. 3, Fig. 13), *Pleurolytoceras dilucidum* (Pl. 3, Figs. 14–17).

- Above, there follow several metres of mudrock that has not been studied.

In the eastern tributary of the Pliensbach the outcrop is more degraded than in the western tributary. In the bank of a small pool, 1.4 m claystones of the Dilucidum-Schichten are exposed. Further up in the creek, these beds crop out again, but are strongly weathered there.

Ammonites: *Leioceras opalinum* β , *Pleurolytoceras dilucidum*.

During a recent flooding event, several slabs of claystone were detached from the floor of the c. 0.5–0.8 m deep water pool. These yielded compressed white-shelled *L. opalinum* α (very common) and *P. torulosum* (= range area of the ‘Torulosum-Knollen’).

Ammonites: *Leioceras opalinum* α var. *buckmani* (Pl. 2, Fig. 11), *L. opalinum* α var. *subglabrum* (Pl. 2, Fig. 10), *Pleurolytoceras torulosum* (Pl. 2, Fig. 9).

In the field notebook of the late W. OHMERT, there is a section from the eastern tributary of the Pliensbach creek dated from June 27th, 1986, in which he noted from the stream bed c. 0.1 m unconsolidated bright yellowish detrital marl with “*fluitans* + *torulosum*” following above c. 0.35 m light grey calcareous marl with an ammonite mass occurrence predominated by *Dumortieria* and “*Pleydellia aalensis*” at the top. From a c. 2 m-thick “lateral slump”, c. 2.5–2.8 m above the bright yellowish marl (later crossed out and replaced by “1.4 m GOTTLIEB (1955)”) he mentioned ammonite-bearing concretions at the base. Above, a 0.2 m thick ammonite accumulation follows comprising compressed, white-shelled “~ *Pl. loth.* – *buckmani*” and a little further up *Lytoceras* cf. *dilucidum*. This means that OHMERT (1993, fig. 2), when compiling his schematic section of the Teufelsloch gorge, in fact illustrated the situation of the nearby Pliensbach creek.

C. Creek bed of the Pliensbach

Ex-situ specimens from the ‘Torulosum-Knollen’ layer (collected from scree; coll. G. GASSMANN) are housed in the collection of the SMNS:

Ammonites: *Leioceras opalinum* α (Pl. 2, Figs. 7, 8), *L. opalinum* α var. *comatum* (Pl. 2, Figs. 2, 3), *L. opalinum* α var. *subglabrum* (Pl. 2, Figs. 4, 5), *Pleurolytoceras torulosum* (Pl. 2, Fig. 1), *P. penicillatum*.

D. Heiningen

Our data on stratigraphy of the former clay pit Mohring in Heiningen (Fig. 3) are based on sections by AL-SAYARI (1970), OHMERT (fieldbook data) and one of us (S.G.). The latter took partial sections in a temporary sewer trench in the southern part of the former clay pit (in 1996) and at the construction of a new building of the company Mayer (in 1998) up to the ‘Torulosum-Knollenlage’. There, OHMERT studied the uppermost parts of the Jurensismergel Forma-

tion. AL-SAYARI (1970) described a section of more than 7 m of claystones following above the Torulosum-Knollenlage.

Jurensismergel Formation

- (at least 0.1 m): Clay-marlstone with jet, belemnites (long, thin) and undetermined ammonites.
- (0.07–0.08 m): Nodular bed of marl-limestone.
- (0.55–0.62 m): Clay-marlstone, partly rich in shell detritus.
- (0.05–0.1 m): Grey bed of marl-limestone, partly nodular, poor in fossils, with two compressed *Cotteswoldia aalensis*.
- (0.05–0.15 m): Detrital, grey clay-marlstone. The transition to the above following claystone is gradational.

Opalinuston Formation (Teufelsloch Member), range area of the ‘Torulosum-Knollenlage’

- (1.9–2.0 m): Dark grey to blackish grey claystone; from 0.7 m above the base onwards with rare dark limestone concretions, mostly lacking fossils, rarely with small nuclei of leioceratids and shell detritus. Two body chambers of lytoceratids have been recorded. In two of the concretions and in the two body chambers, ammonites up to 5.5 cm in diameter occurred. All fossils from this part of the section are preserved with grey shells.

Ammonites: *L. opalinum* α , *Pleurolytoceras penicillatum*.

- (0–0.1 m): Only locally developed lenticular bed developed within the claystones below, greyish-black claystones with white-shelled, compressed fossils. The boundary to the underlying claystone lacking white-shelled fossils is very sharp. The next bed above follows with a very sharp boundary as well. Numerous limestone concretions and lytoceratid body chambers contain three-dimensionally preserved white-shelled fossils.

- (0.12–0.13 m): Greyish-black claystone with accumulation of white-shelled fossils, which are less deformed and compressed than in the lower, locally occurring claystone lenses. Calcareous concretions with white-shelled, three-dimensionally preserved fossils are abundant, but usually smaller than in the claystone lenses below. The limestone concretions have smoother surfaces than those in the claystone lenses below. Lytoceratid body chambers with white-shelled fossils are abundant as well. The concretions often show cracks filled with gypsum which may cut the ammonites inside. Some ammonites are partly dissolved by acidic pore water that later fostered to gypsum precipitation or partial deformation. The fossils in the body chambers of lytoceratids are better preserved, since gypsum occurs only marginally. The fossil content of this continuous bed is the same as in the underlying beds of the Opalinuston Formation.

Ammonites (from both concretion layers and the body chambers): *L. opalinum* α (Figs. 5.15–5.18), *L. opalinum* α var. *arkelli* (Fig. 5.12), *L. opalinum* α var. *arcuatum* (Fig. 5.9), *L. opalinum* α var. *gracile* (Fig. 5.4), *L. opalinum* α var. *tomum* (Figs. 5.5–5.8), *L. opalinum* α var. *angulatum* (Fig. 5.2), *L. opalinum* α var. *buckmani* (Fig. 5.13), *L. opalinum* α var. *undatum* (Fig. 5.1), *L. opalinum* α var. *subcostosum* (Figs. 5.10, 5.11), *L. opalinum* α var. *comatum* (Fig. 5.14), *L. opalinum* α var. *leorum* (Fig. 5.3), *L. opalinum* α var. *subglabrum* (Figs. 4.1, 4.2, 4.4), *L. opalinum* α var. *pseudoaalensis* (Fig. 4.3), *Bredya subinsignis* (Figs. 5.19, 5.20), *Canavarella fasciata* (Figs. 13a–c), *Pleurolytoceras torulosum*, *P. taeniatum*, *P. penicillatum*, *P. dilucidum*.

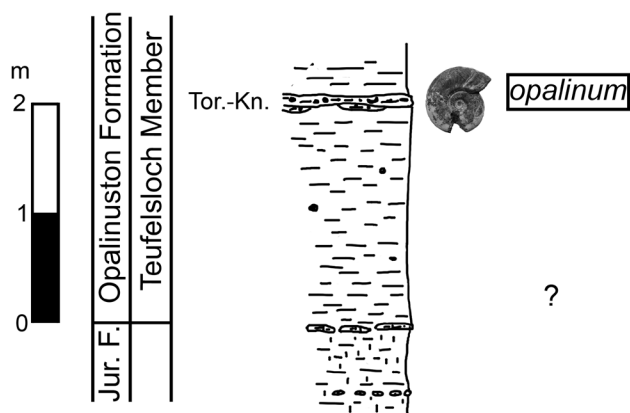


Fig. 3. Section in the transition Jurensismergel Formation / Opalinuston Formation in the former clay pit Mohring in Heiningen. Jur. F. = Jurensismergel Formation; Tor.-Kn. = Torulosum concretion layer.

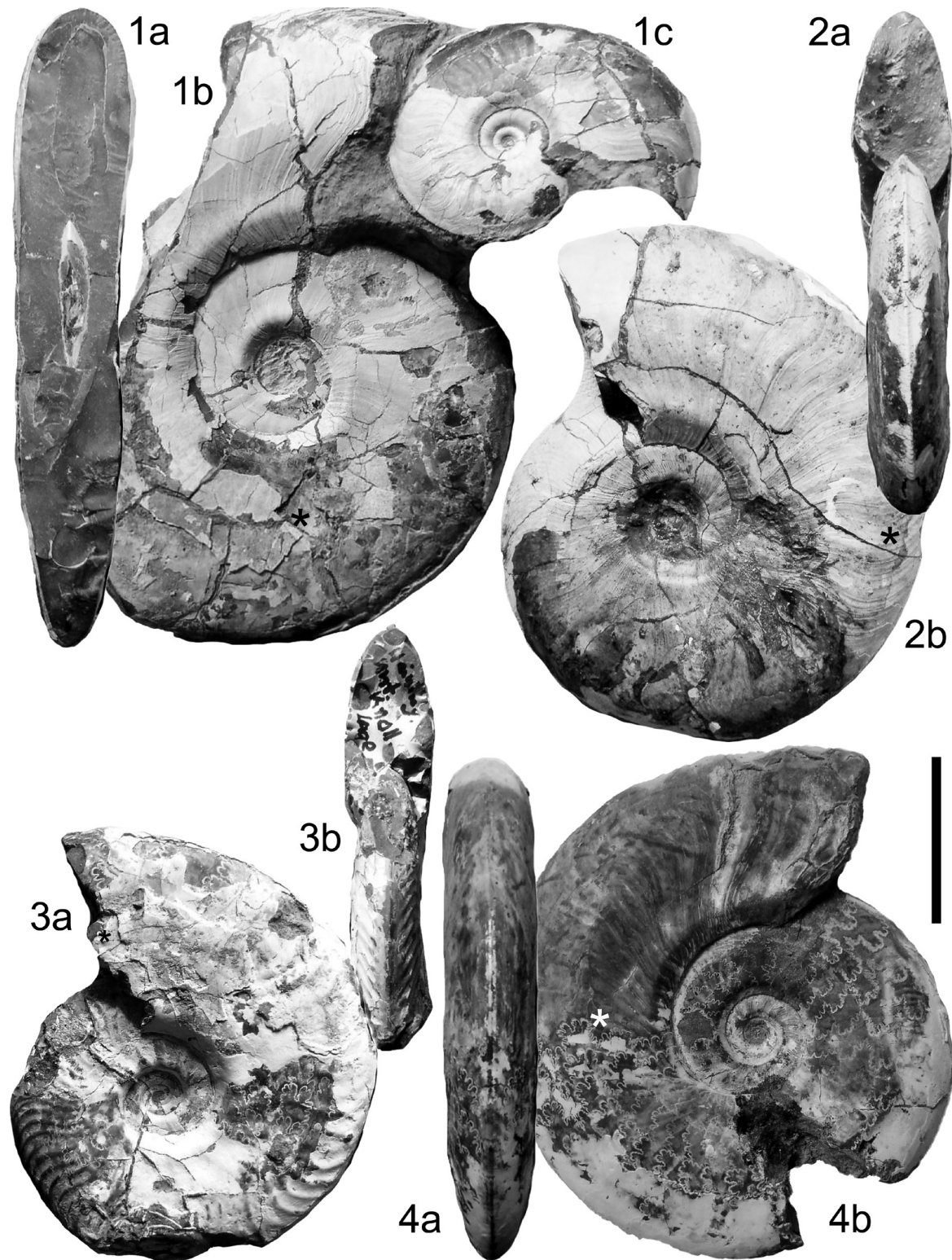


Fig. 4. (1, 2, 4): *Leioceras opalinum* α var. *subglabrum* [M], (1) SMNS 70608/1 (limestone concretion from the upper concretion layer); (2) SMNS 70608/2; (4) SMNS 70608/3. (3): *L. opalinum* α var. *pseudoaalensis* [M], SMNS 70608/4. (1–4) former clay pit Mohring in Heiningen; Opalinuston Formation, Teufelsloch Member, range area of the Torulosum concretion layer; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opalinum* Biohorizon. Ammonites slightly reduced in size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

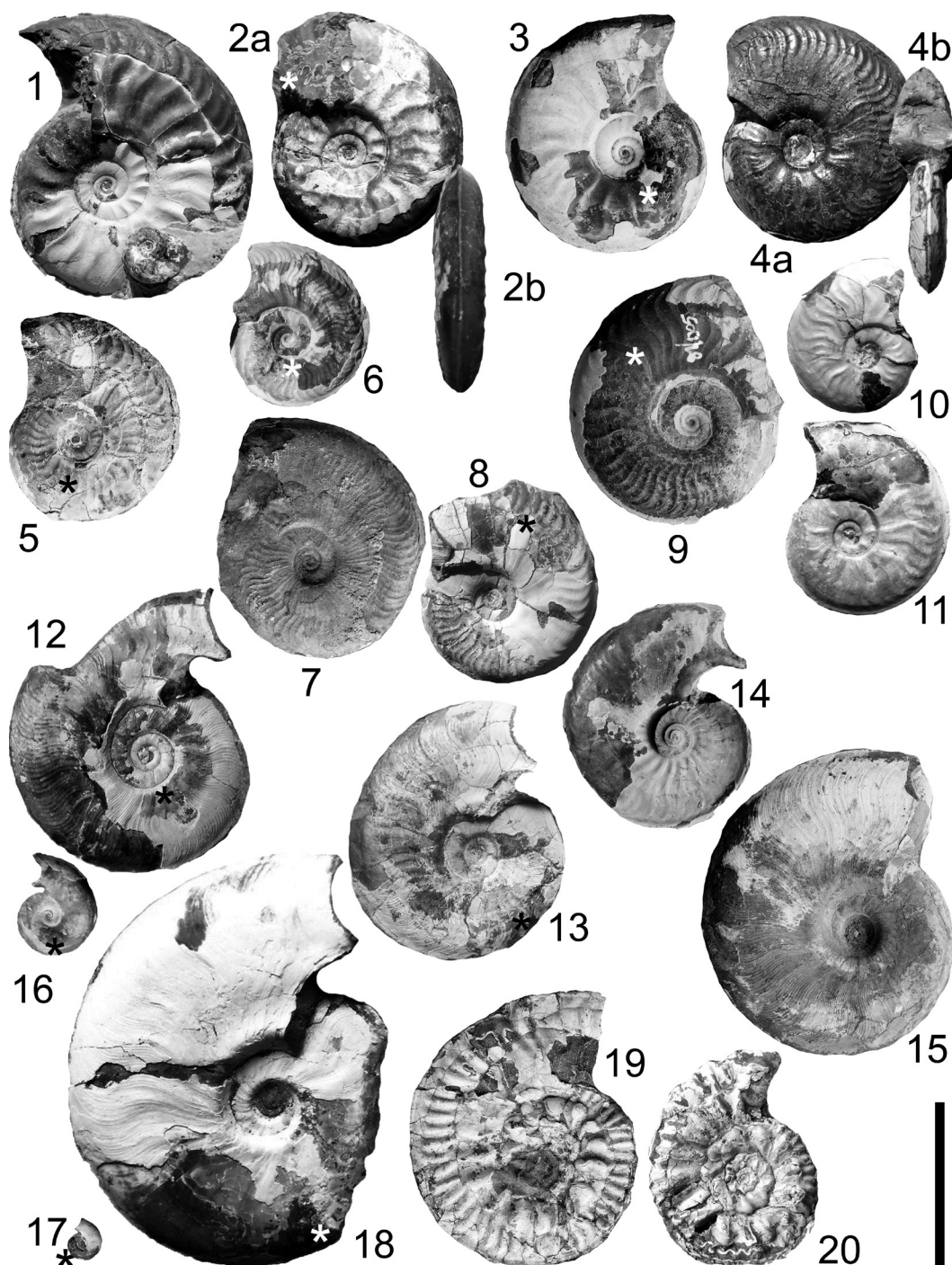


Fig. 5. (1): *Leioceras opalinum* α var. *undatum* [m], SMNS 70608/5. (2) *L. opalinum* α var. *angulatum* [m], SMNS 70608/6. (3) *L. opalinum* α var. *leurum* [m], SMNS 70608/7. (4) *L. opalinum* α var. *gracilis* [m], SMNS 70608/8. (5–8) *L. opalinum* α var. *tomum* [m], (5) SMNS 70608/9, (6) SMNS 70608/10, (7) SMNS 70608/11 (8) SMNS 70608/12. (9) *L. opalinum* α var. *arcuatum* [m], SMNS 70608/13. (10–11) *L. opalinum* α var. *subcostosum* [m], (10) SMNS 70608/14, (11) SMNS 70608/15. (12) *L. opalinum* α var. *arkelli* [m], SMNS 70608/16. (13) *L. opalinum* α var. *buckmani* [m], SMNS 70608/17. (14) *L. opalinum* α var. *comatum* [m], SMNS 70608/18. (15–18) *L. opalinum* α [m], (15) SMNS 70608/19, (16) SMNS 70608/20, (17) SMNS 70608/21 (18) SMNS 70608/22. (19) *Bredya subinsignis* [M], SMNS 70608/23. (20) *Bredya subinsignis* [m], SMNS 70608/24. (1–20) former clay pit Mohring in Heiningen; Opalinuston Formation, Teufelsloch Member, range area of the Torulosum concretion layer; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opalinum* Biohorizon. Ammonites slightly reduced in size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

Beds above the ‘Torulosum-Knollenlage’

Our description of the c. 7 m of beds following above the ‘Torulosum-Knollenlage’ as well as that of HEGELE (1995: 99, profile at right) was compiled from the diploma thesis of

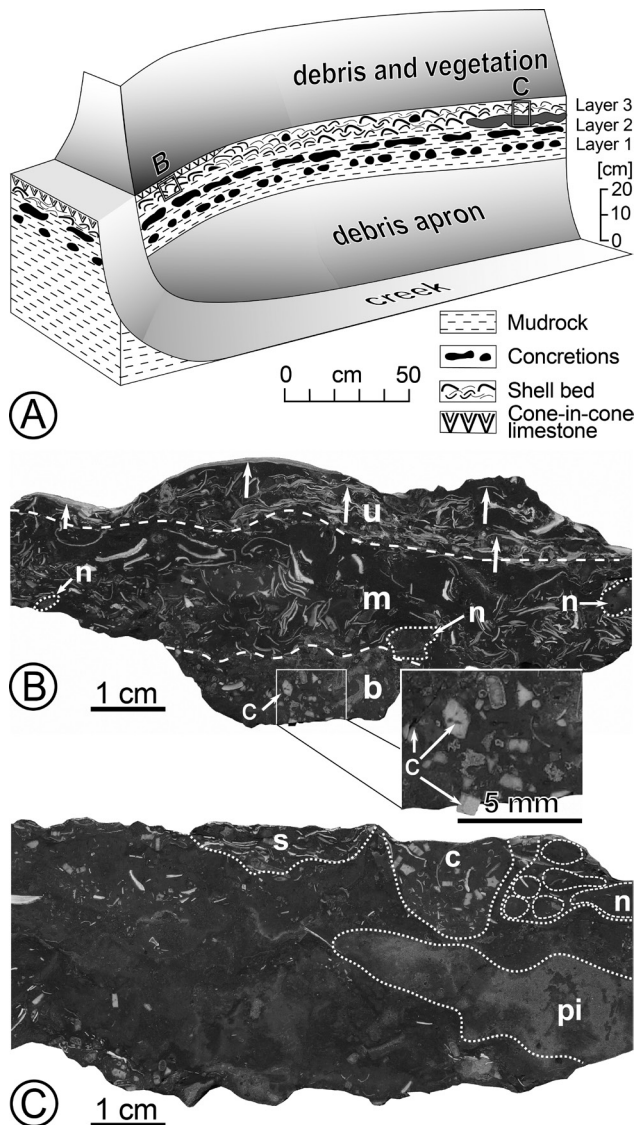


Fig. 6. Lithologic variability of the Lucinenbank (LB; Layer 3) encountered in the Teufelsloch gorge. (A) Schematic drawing of the outcrop in September 2020 and location of the samples (within frame) shown in (B) and (C). (B) Grading of components within the LB having crinoid debris (c) enriched (frame marking the area shown enlarged within the inset, enriched crinoid debris) at the base (b), upright to inclined (fragmented) shells and small nodules (n) in the middle part (m), and densely packed mollusk shells with umbo up (arrow) indicating current-stable position (u). (C) Micritic limestone impregnated by pyrite (pi) with slightly nodular appearance exhibiting crinoid-rich (c), nodular (n), and shell-rich (s) domains (for details see Chapter 8.2).

AL-SAYARI (1970). Above the ‘Torulosum-Knollenlage’, the limestone concretions are rich in fossils and white-shelled fossils become generally scarce. AL-SAYARI (1970) was unable to make a lithological subdivision of the uniform blackish-grey claystones and subdivided the section artificially into 11 horizons, which we refer to with numbers in square brackets. The only recognizable differences are the occurrences of *Bositra* shell fragments in the 3rd and 5th horizon, whereas these are lacking in all other horizons. The determination of the ammonites is after AL-SAYARI (1970). All ammonites from this part of the section are compressed.

- (0.1 m [2]): Blackish-grey claystone, poor in fossils. Rare ammonites (*L. opalinum*, *Pleurolytoceras* “*lineatum*”).
- (0.75 m [3]): Alternation of blackish-grey and medium-grey claystones with shell detritus (*L. opalinum*, *P. torulosum*, *P. “lineatum”*).
- (0.91 m [4]): Blackish-grey, micaceous claystone rich in fossils, with small disc-shaped limestone concretions. In the upper part a level with burrows. Fossils partly accumulated (*L. opalinum*, *P. torulosum*, *P. “lineatum”*).
- (0.6 m [5]): Grey claystone with shell detritus (*L. opalinum*).
- (0.8 m [6]): Black-grey, micaceous, thinly bedded, claystone, rich in fossils (*L. opalinum*, *P. torulosum*).
- (0.72 m [7]): Dark grey, finely bedded claystone (*L. opalinum*).
- (0.5 m [8]): Light? grey claystone, rich in fossils (*L. opalinum*, *P. torulosum*, *P. “lineatum”*).
- (0.7 m [9]): Brownish weathered claystone, rich in ammonites (*L. opalinum*, *P. torulosum*).
- (0.9 m [10]): Light grey, partly silty claystone. In the lower part shell fragments are abundant. Accumulations of ammonites up to 0.4 m in diameter (*L. opalinum*, *L. “costosum”*, *P. torulosum*, “*Hammatoceras subinsigne*”).
- (1.16 m [11]): Bright grey claystone with four levels of siderite concretions, which are mostly, embedded within up to 0.05 m thick calcareous lenses of siltstone. Fossils are rare (*L. opalinum*).

3.1.1.2. Lucinenbank

- (c. 0.1–0.15 m) This dark grey bed forms a small barrier in the stream bed (Fig. 6A), c. 14.5 m below the Pentacrinitenplatte. Some meters below the Lucinenbank, there are several levels with siderite concretions.

The upper and lower extent of the Lucinenbank is bounded by a limestone layer with cone-in-cone structures (WENK 1927; for lithologic-sedimentological details see section 8.2). This bed yields abundant *Mesomiltha* (“*Lucina*”) *plana* (ZIETEN) and other bivalves (QUENSTEDT 1857; GROPPER 1925; HEGELE 1995: 97, fig. 3). The only ammonites from this bed are scarce compressed and deformed leioceratids, mostly preserved with their opalescent shell. At several places, the Lucinenbank is represented by lithified clays (GROPPER 1925). Immediately above the Lucinenbank, there are thin (c. 0.1 m), stronger lithified claystones with numerous white-shelled fossils.

Ammonites: *Leioceras opaliniforme* var. *opalinum* (Fig. 7.1), *L. ex gr. opaliniforme* (Fig. 7.2).

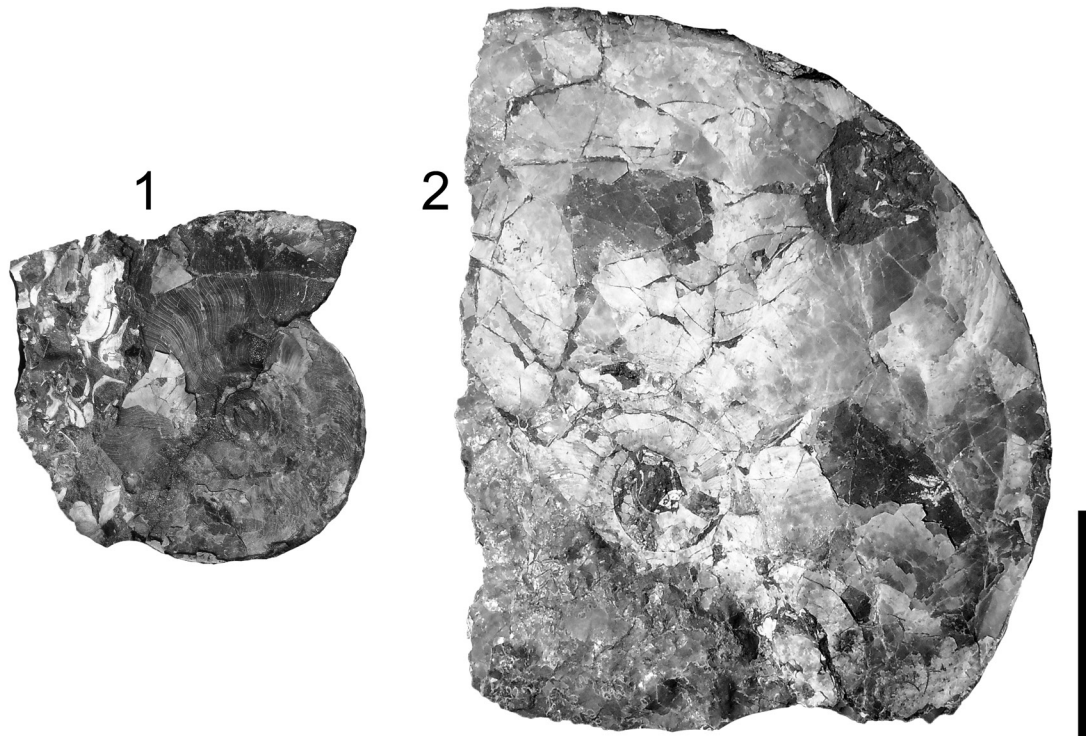


Fig. 7. (1): *Leioceras opaliniforme* var. *opalinum* [m], SMNS 70608/25. **(2):** *L. ex gr. opaliniforme* (BUCKMAN) [M], SMNS 70608/26. (1, 2) Opalinuston Formation, Teufelsloch Member, Lucinenbank; Teufelsklungenbach gorge at Bad Boll-Eckwälden; Lower Aalenian, Opalinum Zone, Opalinum Subzone, ?*opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm.

3.1.1.3. Levels of the ‘Pentacrinitenplatten’

• (c. 5–6 m) Between approximately c. 33 m and 38 m below the top of the Wasserfallschichten and c. 14.5 m above the Lucinenbank there are various layers with mass-occurrences of fragmented columnalia of the crinoid *Chariocrinus wuerttembergicus* (KOBLER 1967, 1972, beds 3–4). In the range of c. 37 m below the top of the Wasserfallschichten there are several lenticular layers of such lithified accumulations (OPPEL 1856–1858; GROPPER 1925; KOBLER 1967, 1972; SIEVERTS-DORECK 1964; HEGELE 1992: figure on p. 345). They yield abundant white shell fragments and small pebbles. Small-sized shells of *Scaphotrigonia* (Pl. 4, Fig. 2) are so common that GROPPER (1925) considered naming these beds ‘Trigoniplatten’. QUENSTEDT (1857) and GROPPER (1925) mentioned fragments of leioceratids as well. During our own studies, we were unable to locate a ‘Pentacrinitenplatte’ layer in the Teufelsklungenbach creek. Despite of intensive searching, we even did not find any loose pieces with crinoid columnalia. In the level of the ‘Pentacrinitenplatten’, however, we recovered a layer of white-shelled leioceratids with diameters of c. 10 cm (Pl. 4, Fig. 3), mostly preserved as fragmentary body chambers. Occasionally, on top of this bed a hardground with numerous crinoid columnalia is developed. During the construction of the motorway A 8 along the Aichelberg slope, a c. 0.05 m thick clay-marlstone was recognized several decametres below the ‘Wasserfallschichten’, probably in the level of the ‘Pentacrinitenplatten’. Within this bed there was a centimetre-thick, strongly lithified claystone layer yielding numerous bivalves and other shell fragments and

fragments of tiny leioceratids besides a *Leioceras ex gr. opaliniforme* var. *plicatum* (Pl. 4, Fig. 1a).

Ammonites: *Leioceras ex gr. opaliniforme* var. *plicatum* (Pl. 4, Figs. 1, 3).

3.1.1.4. Opaliniforme-Schichten (c. 5 m: beds 10–13 of KOBLER 1967, 1972 [= K 10–K 13])

• (~ 2 m): At ~ 21.3 m below the top of the Wasserfallschichten (KOBLER 1967, 1972), there is a c. 2 m thick silt-claystone rich in fossils (bed K 10). About 0.7 m below (in bed K 9) a continuous layer of densely packed, irregular grey limestone concretions up to 5 cm in size occurs, which are locally so densely packed that they constitute a nodular limestone. It is exposed along the creek for several metres and forms a good marker bed. Within bed K 10 occur compressed juvenile leioceratids with a diameter of 3–5 cm; they are especially abundant in the lower part of bed K 10. Additionally, bed K 10 yields abundant *L. opaliniforme* up to 15.5 cm in diameter of which only the body chambers are three-dimensionally preserved, whereas the phragmocones are compressed (Pl. 7, Figs. 1–3; Pl. 8, Figs. 1–3) and rare *Pleurolytoceras dilucidum* (Pl. 8, Figs. 4, 5). In the middle part of bed K 10, three-dimensionally preserved body chambers of leioceratids are remarkably common. About 1.6–1.8 m above the limestone concretion layer of bed K 9, there is a reddish-brown, more silty layer in bed K 10 occasionally containing ‘Opalinusknochen’ with numerous more or less compressed,

mostly microconchiate leioceratids inside. In the same level and c. 0.6–0.8 m higher in the section there are more calcareous concretions as well containing less deformed, mostly microconchiate leioceratids (for lithologic-sedimentological details see section 8.2).

- (1.5 m): Silt-claystones with numerous layers of flat siderite concretions (bed K 11, c. 19.3 to 17.8 m below the top of the ‘Wasserfallschichten’).

- (2 m): In the silt-claystones of beds K 12 and K 13 (c. 1.3 m and c. 0.7 m; after KOBLER c. 17.8 to 16.5 m and 16.5 to 15.8 m below the top of the ‘Wasserfallschichten’) leioceratids are more common again (Pl. 5, Fig. 10; Pl. 9, Figs. 2–6), but still rarer than in bed K 10. Remarkable are juvenile, three-dimensionally preserved leioceratids (Pl. 9, Figs. 3–5; KOBLER 1967, 1972). We recovered only few concretions with leioceratids from the beds K 12 and K 13; one of them yielded numerous strongly compressed, large-sized macroconchiate leioceratids (Pl. 5, Fig. 10). KOBLER (1967, 1972) mentioned a layer of ‘Opalinusknohlen’ in bed K 13, which can be traced along the entire wall of the outcrop. Since these concretions occur in distances of several metres (KOBLER 1967: 105), it depends on temporary outcrop conditions whether or not this layer can be identified. Biostratigraphically, the interval of the Opaliniforme-Schichten cannot be further subdivided.

Ammonites: *Leioceras opaliniforme* (Pl. 5, Figs. 3, 6, 10; Pl. 6, Figs. 8, 11b; Pl. 7, Figs. 1, 2; Pl. 8, Figs. 2, 3; Pl. 9, Figs. 1–7), *L. opaliniforme* var. *hansrieberi* (Pl. 7, Fig. 3; Pl. 8, Fig. 1), *L. opaliniforme* var. *tyrrhenum* (Pl. 6, Figs. 2a, 11d–f), *L. opaliniforme* var. *opalinum* (Pl. 5, Fig. 1), *L. opaliniforme* var. *partitum* (Pl. 5, Figs. 2a, 4a–5, 7–9b, 12b; Pl. 6, Figs. 1, 2b–5, 7, 9–10b, 11a, c), *L. opaliniforme* var. *comatum* (Pl. 5, Figs. 2b–c, 11, Pl. 6, Figs. 12a, b), *L. opaliniforme* var. *subcostosum* (Pl. 5, Fig. 12a, Pl. 6, Figs. 6, 13, 14), *Canavarella fasciata* (Fig. 13.3), *Pleurolytoceras dilucidum* (Pl. 8, Figs. 4, 5).

In his published section, OHMERT (1993: 156; fig. 2) placed the *opaliniforme* Biohorizon c. 30 m below the Wasserfallschichten. The ammonites he recovered from this horizon, however, are partly labelled “c. 470 m NN”. The top of the Wasserfallbank (“Breiter Stein”) lies at an altitude of 491 m above sealevel. Consequently, the beds of the *opaliniforme* Biohorizon occur c. 20 m below the Wasserfallbank. This was confirmed by measurements of KOBLER (1967, 1972) with a leveling instrument. Therefore, the total thickness of the Opalinuston Formation in the Teufelsloch gorge is only c. 130 m, and not 140 m as erroneously stated by OHMERT (1993: fig. 2).

3.1.1.5. Zillhausen Member

Concerning the lithostratigraphical subdivision of the Zillhausen Member, we follow the suggestions by FRANZ & NITSCH (2009). In our description of the section, we additionally refer to data by SÖLL (1954), WEBER (1964), KOBLER (1967, 1972) and OHMERT (1993, and unpublished notes in his field book). The lower boundary of the Zillhausen Member is identified by the onset of fine-sandy silty-claystones or sandy limestone and sandstone beds above the claystones of the Teufelsloch Member (KOBLER 1967, 1972; FRANZ & NITSCH 2009). In the Teufelsloch gorge the base of the Zillhausen Member coincides with the base of the ‘Wasserfallschichten’ (= “Abschnitt C” of KOBLER 1967, 1972; FRANZ & NITSCH 2009: 131). Due to an increase of the silt fraction (mostly quartz) the claystones are more indurated.

A marked increase of the sand content (KOBLER 1967, 1972) occurs slightly higher in the section, approximately coeval with the change from white-shelled aragonitic fossils to brownish calcitic replacement of the shells.

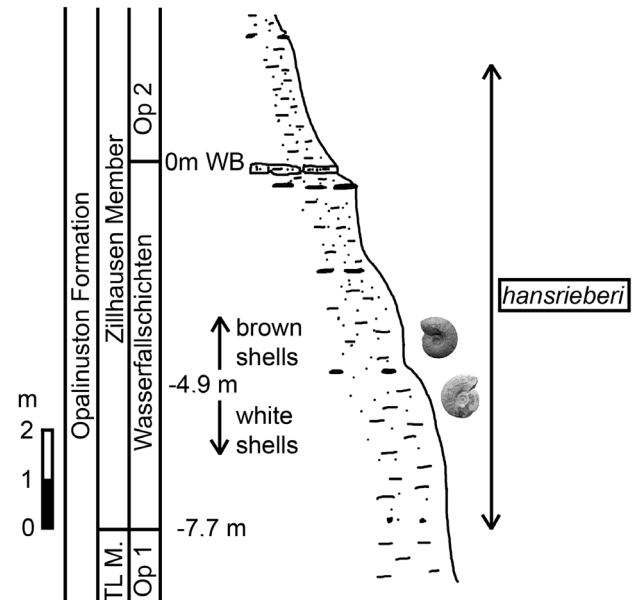


Fig. 8. Section of the Wasserfallschichten (Zillhausen Member) in the Teufelsklängenbach gorge. TL M. = Teufelsloch Member, Op = Opalinuston Formation, WB = Wasserfallbank.

3.1.2.1. Wasserfallschichten

The Wasserfallschichten (Fig. 8; c. 7.7 m) are an alternation of thin beds of calcareous sandstones, sandy limestones, flaser deposits and fine sandy, partly bioturbated silt-clay-marlstones (FRANZ & NITSCH 2009). The higher sand and carbonate contents make the Wasserfallschichten very solid. All concretions of this interval are limestone concretions (KOBLER 1967, 1972). The Wasserfallschichten comprise four stacked bed sets each representing a coarsening-/thickening-upward succession documenting an increase in hydraulic energy having sorted and structured the sediment. Besides an upward-increasing sand content within each bed set, these strata contain exhumed calcareous concretions, which imply sediment reworking that removed a considerable proportion of the (fine) sediment record. The measurements given below refer to the distance with the top of the uppermost bed (= Wasserfallbank) of the Wasserfallschichten. A true waterfall is only present in the uppermost c. 5.6 m of the Wasserfallschichten (see HEGELE 1995: 92; HEGELE 2009: fig. 235).

- (2.2 m): About -7.7 m to -5.6 m (beds 17–18 in KOBLER 1967, 1972). Dark grey, weakly calcareous, firm silt-claystones with numerous white-shelled aragonitic fossils. Besides abundant large-sized leioceratids (Pl. 12, Fig. 2a, b), there is a layer of ‘Opalinusknohlen’ at -7.3 m (KOBLER 1967, 1972; Pl. 10, Figs. 1–6), of which only few could be recovered. In the upper 1.1 m (bed K 18) fossils are rare.

Ammonites: *Leioceras hansrieberi* (Pl. 10, Fig. 7c), *L. hansrieberi* var. *subcostosum* (Pl. 10, Figs. 1, 4, 6, 7a, b), *L. hansrieberi* var. *partitum* (Pl. 10, Figs. 2, 3, 5, 7d, e).

- (0.7 m): About -5.6 m to -4.9 m; dark grey, indistinctly bedded, firm silt-claystones rich in fossils with white shells. At -4.9 m there is an abrupt change in the preservation of fossils from aragonitic white-shelled ones to brown-shelled calcitic ones. About 0.1–0.2 m below this change, there is a layer containing numerous large-sized leioceratids besides trigoniids and other bivalves (for lithologic-sedimentological details see section 8.2).

Ammonites: *Leioceras hansrieberi* (Pl. 11, Figs. 1–3; Pl. 12, Figs. 1–5; Pl. 13, Fig. 1).

- (0.9 m): C. -4.9 m to -4.0 m. Dark grey silt-claystones with exclusively brown-shelled fossils. Approximately 0.2 m above the change from white-shelled to brown-shelled fossils single lithified limey marl layers with ammonites, belemnites and crustaceans occur. Leioceratids are relatively abundant between -4.9 m to -4.6 m and -4.3 m to -4.1 m, but rarer than at the base of the Wasserfallschichten. Large well-preserved *Scaphotrigonia navis* (SMNS 70608/49) are relatively common at c. -4.3 m. In a distance of approximately 50 m further downwards the creek, there is a layer of limestone concretions and a hardground settled by serpulids and bivalves at -4.0 m (SMNS 70608/128).

Ammonites: *Leioceras hansrieberi* (Pl. 14, Fig. 1), *L. hansrieberi* var. *partitum* (Pl. 14, Figs. 2–4), *Tmetoceras scisum* (Pl. 15, Fig. 3).

- (1.2 m): About -4.0 m to -2.8 m; grey-brownish, increasingly fine-sandy silt-claystones, which terminate at -2.8 m in a layer of flat-ellipsoidal limestone concretions (0.03–0.05 m) with rusty weathering crusts. These concretions are embedded in a lithified sandy silt-claystone and form a marked step in the creek bed.

Ammonites: *Leioceras hansrieberi* (Pl. 15, Figs. 1, 2).

- (2.8 m): About -2.8 m up to the top of the Wasserfallschichten; dark grey, platy, slightly fine-sandy silt-claystones with occasional lenses of fine-sandy siltstones. From -2.8 m to -0.9 m dark grey, platy, fine-sandy silt-claystone with irregularly intercalated calcareous concretions (between -2.8 and -1.9 m); a sole ammonite find. At c. -0.9 m, there is a c. 0.2 m thick layer of sandy lime-marlstone concretions forming a prominent step. Above from -0.9 to c. -0.3 m, there are dark grey, platy claystones with several lenses of silt-claystone. The solid grey flaser bed (= Wasserfallbank) at the top of the Wasserfallschichten is 0.25–0.3 m thick and consists of a fine-sandy siltstone with bright limestone concretions.

Ammonites: *Leioceras hansrieberi* (Pl. 16, Fig. 1).

3.1.2.2. Opalinuston 2

- (c. 3.6 m) Sandy, indistinctly bedded silt-claystones, occasionally with layers of limestone concretions, especially in the upper part. At 0.2–0.3 m and c. 2 m above the top of the Wasserfallschichten large, brown-shelled leioceratids occur (Pl. 16, Fig. 2–4; also present in the Riesbach creek: Pl. 17, Fig. 1). Approximately 2.6 m above the top of the Wasserfallschichten, 0.05 m lithified, fine-sandy, weakly calcareous silt-claystone form a small waterfall.

Ammonites: *Leioceras hansrieberi* (Pl. 16, Figs. 2–4), *Leioceras* sp. (0.05 m below belemnite breccia).

3.1.2.3. Belemnite Breccia

- (0.1 m) Grey nodular calcareous marlstone bed with reworked siderite concretions (FRANZ & NITSCH 2009) forming a step in the creek bed. Lenses with numerous belemnite rostra (for lithologic-sedimentological details see below 8.2).

Ammonites: *Leioceras* sp. (“*Ludwig. opalina*” in SÖLL 1954).

3.1.2.4. Opalinuston 3u

- (c. 4–4.2 m) Dark grey, well-bedded silt-claystone very poor in fossils weathering into small rusty pieces. Flat-ellipsoidal siderite concretions with reddish crusts become increasingly abundant towards the top of the bed. Several of these concretions preserve traction-current induced lamination being suggestive of distal tempestites (e.g., WETZEL & ALLIA 2003).

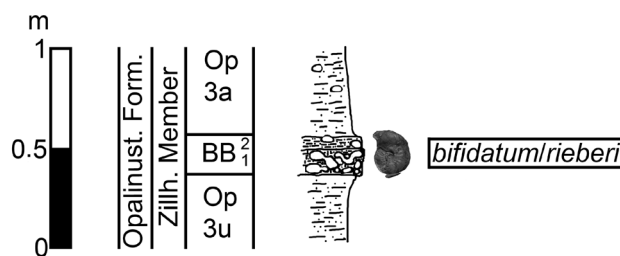


Fig. 9. Section of the Bifidatumbank in the Teufelsklingsbach gorge. Zillh. Member = Zillhausen Member, Op = Opalinuston Formation, BB = Bifidatumbank.

3.1.2.5. Bifidatumbank (= “Costosumbank”)

For a partial section of the Zillhausen Member, see Fig. 9.

- (0.1–0.2 m [BB-1]): The lower lime-marlstone interval bearing nests of chamosite ooids forms a nodular bed, which splits into two partial beds when weathered. In fresh condition, this bed is grey to greenish coloured; its rusty upper side shows a plane, ochre-coloured erosion feature. The micritic nodules exhibit a fuzzy to sharp contact to the host sediment consisting of a greenish-grey wackestone whereas the nodules contain only a few, if any bioclasts and chamositic ooids. Although being suggestive of a bioturbational origin (e.g., KENNEDY & GARRISON 1975), no distinct trace fossils were observed in the nodular beds. Fossils are very rare, only a few, strongly compressed macroconchiate (up to c. 10 cm in diameter) and excellently preserved microconchiate leioceratids have been recovered.

Ammonites: *Leioceras bifidatum* var. *rieberi* (Pl. 18, Fig. 1), *L. bifidatum* var. *partitum* (Pl. 18, Figs. 3–5).

- (0.05–0.1 m [BB-2]): The upper part of the Bifidatumbank is a nodular lime-marlstone (greenish-grey, with enrichments of chamosite ooids) with an ochre-coloured weathering seam. It lies within a grey, partly oolitic clayey marl. In this bed, compressed leioceratids are abundant; other fossils are nautiloids, trigoniids and various other bivalves, and pleurotomariid gastropods. Often the ammonites are attached to the upper surface of the

nodules. The ammonites have a grey colour, which changes to brownish in the weathered state. Within the nodular calcareous marls no ammonites have been recorded.

Ammonites: *Leioceras bifidatum* (Pl. 19, Fig. 4), *L. bifidatum* var. *rieberi* (Pl. 19, Figs. 1, 2), *L. bifidatum* var. *spathi* (Pl. 19, Fig. 5), *L. bifidatum* var. cf. *crassicosatum* (Pl. 18, Figs. 6, 8–10), *L. bifidatum* var. *uncinatum* (Pl. 18, Fig. 7), *L. bifidatum* var. *plicatellum* (Pl. 19, Figs. 3, 6), *L. bifidatum* var. *partitum* (Pl. 20, Figs. 9–10), *L. bifidatum* var. aff. *subcostosum* (Pl. 20, Figs. 13–15a), *L. bifidatum* var. *paucicosatum* (Pl. 20, Fig. 16), *L. bifidatum* var. *striatum* (Pl. 20, Figs. 1–7), *L. bifidatum* aff. *striatum* (Pl. 20, Figs. 8, 11, 12), *Pleurolytoceras* sp. (SMNS 70608/242)

White-shelled fossils, as stated by OHMERT (1993) and FRANZ & NITSCH (2009), have never been recorded in the Bifidatumbank of the Teufelsloch gorge. The Bifidatumbank is present in the Riesbach creek as well, but hardly exposed.

Remarks on the re-naming of the ‘Costosumbank’ as ‘Bifidatumbank’. Coarser-ribbed ammonites from this bed have been traditionally determined as *Leioceras costosum* and the lime-marlstone bed itself was termed ‘Costosumbank’ (e.g., OHMERT 1993; FRANZ & NITSCH 2009). The determination as well as the naming of the bed has to be revised for the following reasons:

(1) The taxon *Ammonites opalinus costosus* QUENSTEDT, 1886 is pre-occupied twice by *Ammonites bucklandi costosus* QUENSTEDT, 1883 and by *A. jamesoni costosus* QUENSTEDT, 1883 and thus, has to be considered invalid (ICZN 2005; CHANDLER & CALLOMON 2009).

(2) The lectotype of *L. costosum* (QUENSTEDT 1886, pl. 55, fig. 20) comes from the vicinity of Gammelshausen, c. 3 kilometres away from the Teufelsloch gorge. It is three-dimensionally preserved with a white aragonitic shell (QUENSTEDT 1886: 447). Ammonites from the Bifidatumbank never exhibit white aragonitic shells like the lectotype of *L. costosum*, but are preserved with a brown calcitic shell. QUENSTEDT’s specimen of *L. costosum* very likely originated from a layer of ‘Opalinusknollen’

at the base of the Wasserfallschichten (see chorotypes Pl. 10, Figs. 4, 6, 7b; RIEBER 1963) and the ribbed ammonites from the Bifidatumbank have been misidentified. Therefore, we use *L. bifidatum* as new index of this lime-marlstone bed.

3.1.2.6. Opalinuston 3o

- (c. 5.5–6 m, see OHMERT 1993, fig. 2) Dark grey, platy silt-claystones lacking fossils, with numerous layers of flattened siderite concretions showing reddish bright-rusty weathering crusts. The three uppermost concretion layers occur at 1.0 m, 0.5 m, and 0.3 m below the lowermost lithified bed of the ‘Zopfplatten’.

3.1.2.7. Level of the ‘Zopfplatten’ (c. 3–3.5 m, see OHMERT 1993, fig. 2)

Fine-sandy irregular siltstone beds and marly fine-sand beds alternate with platy, fine-sandy micaceous claystones (FRANZ & NITSCH 2009). Ripple marks and trace fossils (*Gyrochorte*, *Zoophycos*) are common. These ‘Zopfplatten’ and the fine-sandy siltstones above and below are not precisely definable. For a detailed section, see Fig. 10l.

- (1.5m [ZoP 1]): Alternation of irregular lime-marlstones und marly fine-sandstone beds (= Zopfplatten s. str.).

- (0.42 m [ZoP 2]): Grey, platy silt-claystone.

- (0.2 m [ZoP 3]): Calcareous sandy twin-bed (0.05 m and 0.09 m, respectively) with intercalated grey claystone (0.06 m).

- (0.65–0.7 m [ZoP 4]): Grey, laminated silt-claystone with rare limestone concretions.

- (0.25–0.45 m [ZoP 5] = “Gerölllage” in WEBER (1964): grey, platy, micaceous claystone with greyish-black, partly micaceous, rarely chamositic, ellipsoidal fine-sandy limestone nodules (diameter 0.05–0.12 m, max. up to 0.4 m), which may form a network and occasionally yield ammonites (for lithologic-sedimentological details see below 8.2). Additionally, there occur larger, more irregularly shaped concretions with higher carbonate content and a rough surface, which yield ammonites, numerous bivalves and brachiopods. In a part of the studied outcrop, however, concretions are almost absent. The claystones yield numberless millimetre-thick limestone scales, rarely with compressed, undeterminable leioceratids. Occasionally, especially towards the base of the bed, platy grey-blackish fine-sandy layers with a maximum thickness of eight centimetres occur. They yield numerous ichnofossils; other fossils have not been recorded.

Ammonites: *Leioceras uncinatum* (Pl. 21, Figs. 1–4), *L. uncinatum* var. *stephanovi* (Pl. 21, Fig. 5, Pl. 22, Fig. 6), *L. uncinatum* var. *bifidatum* (Pl. 22, Figs. 1, 2), *L. uncinatum* var. *plicatellum* (Pl. 22, Figs. 3, 4, 7, 8a, 8e), *L. uncinatum* var. *plectile* (Pl. 22, Fig. 5), *L. uncinatum* var. *partitum* (Pl. 23, Figs. 10–11, 14, 15), *L. uncinatum* var. *subcostosum* (Pl. 22, Figs. 8c, d, Pl. 23, Figs. 3, 4, 9, 13, 18), *L. uncinatum* var. *striatum* (Pl. 22, Fig. 8b; Pl. 23, Figs. 16–17, 19–23), *L. uncinatum* var. *paucicosatum* (Pl. 23, Figs. 1, 2, 5–8).

- (0.35–0.5 m [ZoP 6]: At the base (0–0.14 m = ZoP 6a), there is a hard and mostly continuous grey-blackish micaceous calcareous fine-sand bed (~0.08 m) having rare leioceratids and

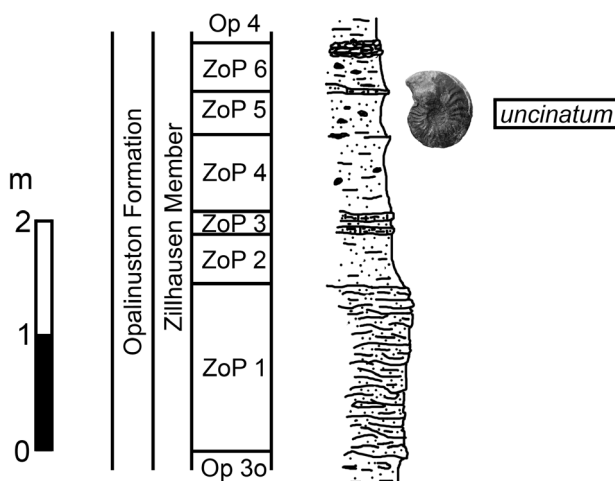


Fig. 10. Section of the ‘Level of the Zopfplatten’ in the Teufelsklungenbach gorge. Op = Opalinuston Formation, ZoP = Level of the Zopfplatten’.

small-sized bivalves in the lower part. Above, a grey-blackish micaceous sandy clay-marlstone (0.25 m = ZoP 6b) follows, occasionally with limestone concretions or platy calcareous fine-sandstone layers at the base. The top is formed by a brown/greenish limestone (0.18 m = ZoP 6c), made up of limestone concretions within a strongly lithified siltstone. The concretions contain chamosite. They have a grey core; at the surface they are brownish or greenish. Above bed ZoP 6a, thin (max. 0.03 m thick) platy calcareous fine-sand layers or grey, sandy limestone nodules may occur.

Ammonites (ZoP 6a): *L. uncinatum* var. *partitum* (Pl. 23, Fig. 12), *L. uncinatum* var. *subcostosum* (Pl. 23, Fig. 13), *L. uncinatum* var. *paucicostatum* (Pl. 23, Fig. 8).

Already WEBER (1964) recorded ammonites determined as “*L. comptum*” in the upper part of the ‘Zopfplatten’ in the Riesbach creek.

3.1.2.8. Opalinuston 4 (c. 6.6 m)

- Dark grey, sandy flaser claystones with concretion layers; no fossils recorded.

- (3.7–3.8 m [Op 4a]): Grey, platy claystone with several layers of grey limestone nodules with brown crusts at 1.1 m above the base, at 1.5 m larger septaria-like concretions with small brachiopods, at 2.2 m limestone concretions with septarian cracks, and at 2.7 m a twin-layer with flat or nodular concretions. In the uppermost metre several thin calcareous layers in irregular positions.

- (0.2 m [Op 4b]): At the bottom a grey solid limestone (0.1 m) with *Chondrites* and other burrows; merged with a lithified claystone, in its top rarely with small calcareous lenses.

- (0.35 m [Op 4c]): Grey, platy fine sandy siltstones, rarely with small limestone concretions.

- (0.35 m [Op 4d]): At the basis, locally containing hard nodules, partly forming a grey limestone; above, there are 0.05 m platy siltstones having a layer of grey limestone concretions at the top.

Ammonites: *Leioceras* sp.

- (2.0 m [Op 4e]): At the basis (0.6 m) a platy grey claystone with irregularly enclosed limestone concretions (0.03–0.05 m). Above a continuous grey limestone (0.03–0.05 m) follows that in turn is overlain by 1.35 m of a very hard, grey, fine-sandy siltstone, with a sandy lime-marlstone bed (0.05 m) c. 0.3 m below the top.

3.2. Achdorf Formation

By definition, the Achdorf Formation coincides with the base of the “Comptumbank” (FRANZ & NITSCH 2009), which is here re-named as Wilflingen-Bank. This bed is recorded from the Western Swabian Alb (RIEBER 1963) to a few kilometres east of the village of Gammelshausen (FRANZ & NITSCH 2009, fig. 7). Since the lower Donzdorf-Sandstein, which forms the base of the Eisensandstein Formation, occurs a few metres above the Wilflingen-Bank, the Achdorf and Eisensandstein formations are intergrad-

ing at their boundary in the study area (FRANZ & NITSCH 2009, fig. 7).

The reason for re-naming the “Comptumbank” as Wilflingen-Bank is based on a new interpretation of the previous index species *Nautilus comptus* REINECKE, 1818. The syntypes of this species have been identified by E. MÖNNIG (Coburg), and as a consequence, it became clear that they represent *Pleydellia* from the Aalensis Zone of the Upper Toarcian. The discovery of the original material makes the neotype designation of a specimen illustrated in DORN (1935: pl. 26, fig. 3) by ZEISS (1972) invalid (ICZN 1999, Art. 75.8). CHANDLER & CALLOMON (2009) designated the specimen illustrated by REINECKE (1818: pl. 1, figs. 5, 6) as the lectotype of *Pleydellia compta*.

Here we introduce the name Wilflingen-Bank as a replacement name for the former “Comptumbank”. Its type locality is a permanent exposure along the road connecting Wilflingen and Gosheim (Wilflinger Steige) in the district of Wellendingen-Wilflingen (DIETL & RIEBER 1980). The “classical” outcrops (Katzensteige) at the steep northern and eastern slopes of the ‘Hirnwiesen’ near Gosheim and some further outcrops at the southern slope of the ‘Hirnwiesen’ (FISCHER 1924; LÖRCHER 1934, 1939; RIEBER 1963) are located in the same district, but are very difficult to access.

The numbering of the beds AF-1 to AF-5 is purely informal. Following OHMERT (1993) and FRANZ & NITSCH (2009), we restrict the term ‘Wilflingen-Bank’ in the study area to the bed of isolated nodules c. 0.9 m below bed AF-2, whereas we include deeper beds and layers with limestone concretions in bed Op-4. A detailed section of the transition between the Teufelsloch and Achdorf formations is provided in Fig. 11.

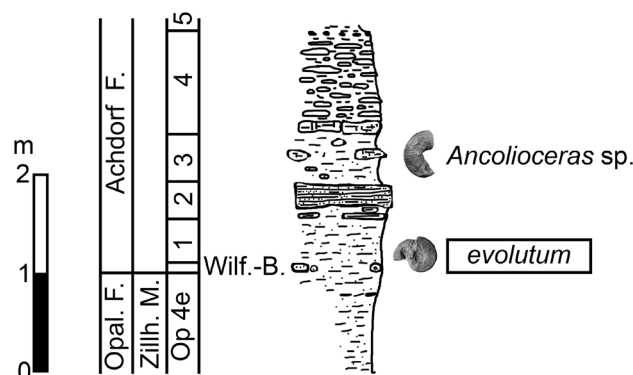


Fig. 11. Section of the transition Opalinuston Formation / Achdorf Formation in the Teufelsklingsenbach gorge. Opal. F. = Opalinuston Formation, Zillh. M. = Zillhausen Member, Op = Opalinuston, Wilf.-B. = Wilflingen-Bank.

3.2.1. Wilflingen-Bank (0–0.1 m)

The very compact, grey, fine-sandy siltstones yield irregular lenses of brown lime-marlstone (0.05–0.08 m) with body chambers or, more rarely, complete leioceratids. Occasionally, such body chambers occur as well in the siltstones. Every 1–2 m there is a hard calcareous marl nodule with blackish cortex and numerous mostly small-sized leioceratids and abundant bivalve shell detritus. The lenses or nodules containing ammonites occur at c. 0.9 below the top of the above following platy limestone bed. The lithology and position in the section fits well with the Wilflingen-Bank exposed at the Aichelberg slope of the motorway A 8. OHMERT (1993) estimated that the bed with limestone concretions containing leioceratids is encountered c. 4 m above the 'Zopfplatten'. This value must be corrected; in fact, this bed occurs in a vertical distance of c. 6.6 m. WEBER (1964) mentioned the Comptumbank, now Wilflingen-Bank, as being rich in ammonites nearby at Gammelshausen, where it is located c. 6 m above the 'Zopfplatten'.

Ammonites: *Leioceras evolutum* var. *striate* sensu CONTINI (Pl. 24, Figs. 6–8, Pl. 25, Figs. 2, 3b–5), *L. evolutum* var. *subcostate* sensu CONTINI (Pl. 24, Fig. 5), *L. evolutum* var. *costate* sensu CONTINI (Pl. 24, Fig. 4; Pl. 25, Figs. 1, 3a), *L. evolutum* var. *crassicosatum* (Pl. 24, Figs. 2, 3), *L. evolutum* var. *comptocostatum* (Pl. 24, Fig. 1), *L. evolutum* var. *striatum* (Pl. 25, Figs. 6b, 9–12), *L. evolutum* var. *paucicosatum* (Pl. 25, Figs. 6a, 7, 8).

3.2.2. Beds above the Wilflingen-Bank (c. 2 m studied)

- (0.5–0.6 m [AF-1]): Grey, hard, fine-sandy siltstones, like below the Wilflingen-Bank, with several lithified domains, occasionally small grey limestone concretions.

- (0.3–0.5 m [AF-2]): An overhanging grey, solid calcarenite bed (0.3 m), in weathered state splitting into 3 to 4 individual layers. Below this massive bed grey, fine-sandy siltstones may occur. At several places, the base of this bed is formed by a few centimetres thick platy calcarenite.

- (0.6 m [AF-3]): Grey siltstone, in the lower 0.4 m occasionally containing grey limestone concretions with brown weathering barks. These concretions yield bivalve detritus, small bivalves and rare fragments of *Ancolioceras* and ?*Leioceras* sp. At 0.3–0.4 m above the base, there is a layer with abundant, mostly compressed *Ancolioceras* sp., ?*Leioceras* sp. and belemnites. In the interval of 0.4–0.45 m lenses of fine-sandy grey to brownish calcareous siltstones; the leioceratids occur in calcareous nodules within these siltstones. At the transition between these lenses and the siltstone, fragments of uncompressed body chambers of *Ancolioceras* sp. occur. Above, the section continues with grey silt-claystones (0.15 m) with a lenticular grey limestone bed just below the massive limestone at the top.

Ammonites: *Ancolioceras opalinoides* (Figs. 12.1–12.3, 12.5–7, 12.9, 12.11, 12.12, 12.14–12.16), ?*Leioceras* sp. (Figs. 12.4, 12.8, 12.13).

- (0.4 m [AF-4]): At the base (0.1–max. 0.15 m), a grey, massive limestone covered by 0.2 m brown fine-sandy flaser siltstones with numerous irregularly bedded grey limestone layers and nodules. The top is formed by 0.08–0.1 m brown, fine-sandy flaser siltstones, in its topmost 0.05 m containing numerous brown/reddish weathered chamositic nodules.

- (0.1 m exposed [AF-5]): Grey, loamy claystones, overlain by Holocene slumped material.

A. Transition Opalinuston / Achdorf Formation at the 'Grünbrücke'

At the Aichelberg slope of the motorway A8, a partial section is well exposed above the 'Grünbrücke'. The southern embankment shows the interval from the Zopfplatten up to the beds above the Wilflingen-Bank (DIETL 2013). Interestingly, the individual beds vary laterally considerably in thickness.

Opalinuston Formation (Zillhausen Member)

Level of the Zopfplatten (~2–3 m): Not studied.

Opalinuston 4 (in total c. 5–6 m):

- (~3–4 m): Not exposed.
- (0.25 m): Grey brown, massive limestone with marly cover, partly more marly or disintegrated into nodules.

Ammonites: *Leioceras evolutum* var. *crassicosatum* (SMNS 70608/243).

- (1.9–2.2 m): Grey, fine-sandy siltstones; 0.4 m grey fine-sandy siltstones overlain by two layers of limestone concretions (0.03–0.05 m each) with intercalated grey fine-sandy siltstones (0.05–0.08 m); further up, there are 0.7 m grey fine-sandy siltstones; then two platy calcareous beds (0.2 m), of which the lower one is continuous; the top is constituted by 0.4–0.7 m of grey fine-sandy siltstones.

Achdorf Formation

- (0.2–0.3 m): Wilflingen-Bank: At the base, a brownish bed disintegrated into nodules (0.05–0.08 m) with mostly compressed ammonites and few shell detritus. The grey sand-marlstone between the nodules occasionally yields body chambers of ammonites; above, there are 0.1–0.2 m grey sandy siltstones and a remarkably brown, partly lithified marl layer (0.1–0.15 m thick). In distances of c. 1.0–1.5 m egg-shaped or flat-ellipsoidal grey limestone nodules (max. 0.15 m in diameter) with thin brownish to dark grey weathering crusts occur. Some of these nodules yield shell detritus and numerous broken, but uncompressed ammonites, however, most of them lack any fossils.

Ammonites: *Leioceras evolutum* var. *striate* sensu CONTINI (Pl. 26, Figs. 7–12), *L. evolutum* var. *subcostate* sensu CONTINI (Pl. 26, Figs. 4–6), *L. evolutum* var. *costate* sensu CONTINI (Pl. 26, Figs. 1–3), *L. evolutum* var. *striatum* (Pl. 25, Figs. 19–22, 23b–25), *L. evolutum* var. *paucicosatum* (Pl. 25, Figs. 13–18, 23a).

- (0.2–0.3 m): Grey, sandy marl.
- (0.3–0.6 m): Several platy, fine-sandy siltstone layers; partly forming a single massive siltstone bed in the top.
 - The beds higher up are almost completely covered by scree now. Ammonites (a loose specimen found directly above the platy siltstone layer): *Ancolioceras opalinoides* (Fig. 12.10).

4. Description of the ammonite fauna

In the studied sections, the ammonite fauna of the Opalinuston Zone is predominated by *Leioceras*, which is by far the most common genus in every bed of the Opalinuston

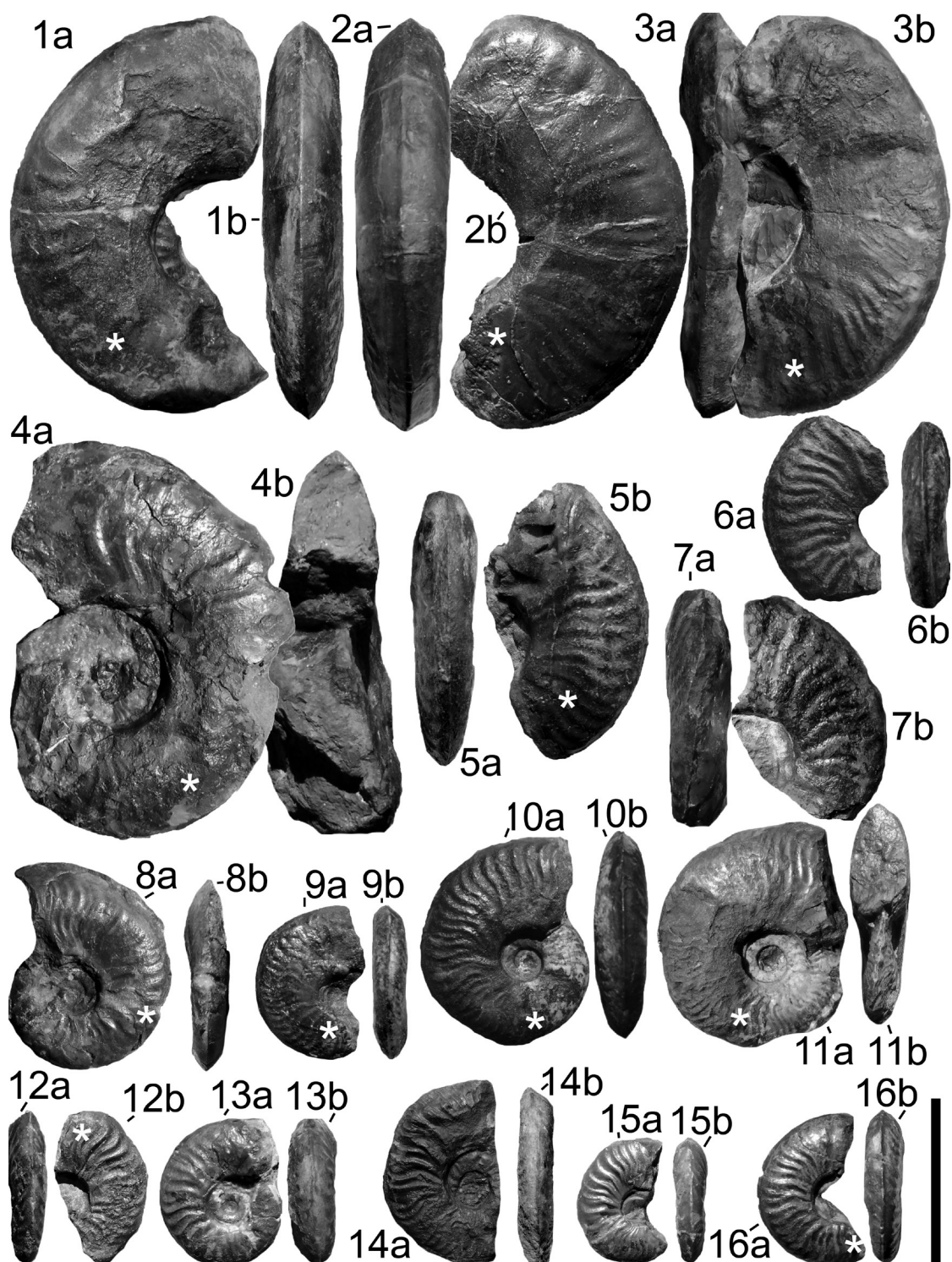


Fig. 12. (1–3, 5–7, 9–11): *Ancolioceras opalinoides* [M], (1) SMNS 70608/27, (2) SMNS 70608/28, (3) SMNS 70608/29, (5) SMNS 70608/30, (6) SMNS 70608/31, (7) SMNS 70608/32, (9) SMNS 70608/33, (10) SMNS 70608/34, Grünbrücke at the motorway A8 at the Aichelberg, (11) SMNS 70608/35. (4) *?Leioceras* sp. [M], SMNS 70608/36. (8, 13) *?Leioceras* sp. [m], (8) SMNS 70608/37, (13) SMNS 70608/38. (12, 14–16) *Ancolioceras opalinoides* [m], (12) SMNS 70608/39, (14) SMNS 70608/40, (15) SMNS 70608/41, (16) SMNS 70608/42. (1–9, 11–16) Teufelsklingenbach gorge. (1–16) Achdorf Formation, bed AF-3; Upper Aalenian, Murchisonae Zone, Haugi Subzone. Ammonites slightly reduced in size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

Formation. Only in the basal part of this formation, ammonoids of the genus *Pleurolytoceras* are relatively abundant as well, and *Pleurolytoceras torulosum* serves as an index of the youngest Subzone of the Toarcian. Rarely, *Pleurolytoceras* ranges higher up into the Opalinum Zone. Besides *Leioceras*, the very rare genus *Canavarella* belongs to the subfamily Leioceratinae as well. Only a few specimens of *Hypophylloceras*, *Tmetoceras* and *Bredya* have been recorded from the Opalinuston Formation of the study area. *Erycites* is extremely rare in the Teufelsloch Member of the entire Swabian Alb and Franconia (QUENSTEDT 1886; ETZOLD et al. 1989; SCHWEIGERT 1996; SCHULBERT 2001; DIETZE & SCHWEIGERT 2016), and it has not yet been recorded in the study area. In the claystones of the *opaliniforme* and *hansrieberi* biohorizons and in the *bifidatum/rieberi* Biohorizon, ammonites are preserved as “pressure shadow concretions” (sensu SEILACHER et al. 1976).

4.1. Genus *Leioceras* HYATT, 1867 (Family Graphoceratidae BUCKMAN, 1905, Subfamily Leioceratinae SPATH, 1936)

Type species: *Nautilus opalinus* REINECKE, 1818.

Remarks on the genus *Leioceras*: We refrain from splitting leioceratids according to various conch characters (ribbing style, involution, whorl section, adult size etc.) into morphologically defined (sub-)genera, e.g., *Leioceras*, *Cylicoceras*, *Cypholioceras* etc. (see BUCKMAN 1887–1907; CONTINI 1969; CONTINI et al. 1997; CHANDLER 1997). The specimens from all studied beds are highly variable and do not allow any delimitations between such morphogenera. As a consequence, we include almost all leioceratids in the single phylogenus *Leioceras* (e.g., RIEBER 1963; URETA GIL 1983; CHANDLER & CALLOMON 2009; CHANDLER et al. 2012; CHANDLER 2019). In contrast, HOWARTH (2013) included in the Leioceratinae the genera *Leioceras* HYATT, *Canavarella* BUCKMAN and *Cylicoceras* BUCKMAN. We partly concur, because some very evolute specimens with a remarkably falcoid ribbing style do not fall into the variation of the genus *Leioceras* and are included here in *Canavarella* (see Chapter 4.3.2).

4.1.1. Comments on the species concept

All leioceratids of the genus *Leioceras* in the study area are treated as a succession of chronospecies. The same concept has been successfully applied in our revisions of the genera *Phlycticeras* (SCHWEIGERT et al. 1998), *Garantiana* (DIETZE et al. 2002), *Sonninia* (DIETZE et al. 2005), *Strigoceras* (SCHWEIGERT et al. 2007) as well as in the description of the genus *Brasilina* in the Upper Aalenian of the Geisingen clay pit (DIETZE et al. 2014). A similar concept was already used by HOFFMANN (1913) for the description of the Late Aalenian leioceratids of Sehnde near Hannover. An indispensable basis for this species concept is a sufficient number of bed-by-bed collected

adult specimens (CHANDLER & CALLOMON 2009). This allows studying the variation in succeeding populations. Indeed, in every studied time slice, the genus *Leioceras* shows a great intraspecific variation, with all possible combinations of characters. Traditionally, these varieties have been often treated as morphospecies having a vertical range or even as different morphogenera (e.g., *Leioceras* [m] – *Costiceras* [m] – *Cypholioceras* [M] – *Cylicoceras* [M]). Studying ammonite populations in their stratigraphical succession indicates that the evolution of the genus *Leioceras* from the Torulosum Subzone (Aalenian Zone, Upper Toarcian) until the end of the Opalinum Zone (Lower Aalenian) is a chronocline (CHANDLER & CALLOMON 2009; CHANDLER et al. 2012; CHANDLER 2019). The range of variation of the ammonite populations differs in each time slice. Some conservative morphologies can have vertical ranges across several time slices. Each chronospecies represents a sole population or generations of populations within the chronocline of *Leioceras*. Within the c. 130 m thick Opalinuston Formation leioceratids are not continuously present, but concentrated in a few, mostly thin intervals, and they are very rare or missing in the remaining parts of the section. Therefore, the individual chronospecies represent only short, unequal segments of a continuous evolution. The unrecorded time makes them fairly well distinguishable from each other. Hence, a chronospecies is defined – analogous to a biological species – by the characters of a reproductive population and their isolation from other contemporaneous populations (CALLOMON 1985; MAYR 2000; DIETZE et al. 2005).

How can this species concept fit with the rules of nomenclature? In the optimal case, the name of a leioceratid ammonite should imply (1) the chronocline, (2) the chronospecies and (3) the morphological characters. WAAGEN (1869) was the first to suggest a solution, which, however, was rejected because of its complexity (WILLMANN 1985; DIETZE et al. 2005). WAAGEN (1869) concurrently named (1) the chronocline (WAAGEN: “Formenreihe” or “Collectivart”), (2) the evolutionary position within this chronocline (WAAGEN: “Mutation”), the chronospecies, and (3) the morphological characters of the individual ammonite (WAAGEN: “Varietät”). We here follow this concept, with some practical modifications:

(1) The genus (here *Leioceras*) implies an assignment to a phylogenus, in contrast to traditionally used morphogenera (DIETZE et al. 2005).

(2) As a chronospecies, the species name informs about the stratigraphical age of the specimen. In the fossil record, it cannot be proven whether or not a population constituted a reproductive community. The only available criteria are morphological characters and their simultaneous occurrence, at least at a geological scale. Hence, the chronospecies concept is applied for a practicable handling. A single population or a succession of populations

with indistinguishable variations (= fully intergrading morphological characters) represents the chronospecies. The duration of a chronospecies can be restricted to a single biohorizon; in this case the chronospecies corresponds to a palaeobiospecies (DIETZE et al. 2002; CHANDLER & CALLOMON 2009). However, its duration may exceed a complete ammonite biozone or even longer (SCHWEIGERT et al. 1998, 2007). We have to accept some subjective criteria for the discrimination of individual chronospecies. However, according to the principle of priority (ICZN 1999), the oldest published name has to be used for the chronospecies (DZIK 1990). The same principle applies for the naming of the phylogenus (see CHANDLER 2019) – in leioceratids *Leioceras* HYATT, 1867 has priority. Since the exact type horizons of many leioceratid taxa are unknown, a possible solution could be to introduce newly defined chronospecies with well-known type horizons (e.g., *Leioceras comptocostosum* CHANDLER & CALLOMON, 2009). However, that procedure is hardly acceptable and would increase the number of abiological taxa. The most practicable solution for naming the chronospecies is searching for an already existing taxon definitely coming from the range of the studied interval and not representing an extreme variety. This concept allows a continuous use of traditional taxa.

(3) The morphology of a specimen can be indicated as a variety (“var.”), which is not affected by the strict rules of the ICZN (1999, Art. 45.5). The type horizon of the taxon, on which this variety is based, must not necessarily coincide with the type horizon of the respective chronospecies, and the same variety may be used in different chronospecies. If the morphology of a specimen corresponds to the type of the respective chronospecies we do not speak of a variety.

In practice, we slightly modified the procedure suggested by DIETZE et al. (2005). As an example, *Leioceras opalinum* (REINECKE, 1818) var. *subglabrum* ex BUCKMAN, 1902 sp. (1) is a specimen belonging to the chronocline of *Leioceras*, (2) it comes either from the *opalinum* Biohorizon or from the *dilucidum* Biohorizon, (3) and morphologically, it corresponds to *L. subglabrum*. In short: *Leioceras opalinum* var. *subglabrum*. In the very special case of the chronospecies *Leioceras opalinum*, we further distinguished an α -form and a β -form. The reason is that the populations of the *opalinum* and *dilucidum* biohorizons slightly differ with respect to a higher proportion of involute forms in the *dilucidum* Biohorizon, especially in microconchs. However, since an increase of the adult size of macroconchs, which is an important evolutionary character, is not recorded, we separated only an α -form and a β -form, *L. opalinum* α und *L. opalinum* β , instead of two chronospecies, followed by the morphological variety.

A higher number of varieties within a chronospecies does not necessarily imply a greater variation. The higher

number of described varieties mainly results from a historical focus of studies on special beds or intervals. This is the case in the transition Toarcian/Aalenian or in the Bifidatum Subzone. In contrast, only few morphospecies exist for ammonites from the top of the Opalinum Subzone. To avoid an inflation of purely artificial taxa, we did not erect additional morphospecies, but we gave the existing varieties a broader definition. In the case of ammonites from intervals with more described morphospecies, we used these names for a better characterization of the morphological diversity.

4.1.2. Relationships between *Leioceras* HYATT, 1867 and *Pleydellia* BUCKMAN, 1899

The phylogenus *Leioceras* evolved from the phylogenus *Pleydellia* of the latest Toarcian. The respective type species of both genera, *Nautilus opalinus* REINECKE, 1818 and *Pleydellia comata* BUCKMAN, 1899, differ only little from each other. The types of both taxa mainly differ by a slightly wider umbilicus and a broader whorl section in *P. comata*. In the basal Opalinum Subzone, there is an overlap of both genera (OHMERT 1993; CONTINI et al. 1997; CRESTA et al. 2001; SCHULBERT 2001). Following our chronospecies concept, we assign ammonites of the Opalinum Subzone with a *Pleydellia*-like morphology to varieties of *L. opalinum*. Although the apportionment of genera within a chronocline is arbitrary, we favour a division at the Toarcian/Aalenian stage boundary. Taking *Pleydellia* as a junior synonym of *Leioceras*, the genus *Cotteswoldia* BUCKMAN, 1902 should also be included (HOWARTH 2013).

4.1.3. The chronospecies of *Leioceras* and its varieties in the succession of ammonite biohorizons

4.1.3.1. *opalinum* Biohorizon (range area of the Torulosum-Knollen)

***Leioceras opalinum* (REINECKE, 1818)** [HT: *Nautilus opalinus* REINECKE, 1818, p. 55, figs. 1, 2; photographs in OHMERT & ROLF 1994 and SCHULBERT 2001; re-figured herein on Pl. 3, Fig. 1].

The holotype of this species comes from near Altenbanz in the northern Franconian Alb (REINECKE 1818: “versus montem Steglitz”), probably from the vicinity of the hamlet Neuhof (HOFFMANN 1970; ZEISS 1972). The long missing specimen, a phragmocone with a diameter of 42 mm, was re-discovered in Coburg by E. MÖNNIG. This rediscovery was obviously unknown to HOWARTH (2013), who did not mention this important specimen. Based on its preservation, its morphological characters and the presumed type locality, it must originate from the basal part of the Opalinuston Formation (OHMERT 1993). It is unclear whether the holotype is a microconch (SCHULBERT 2001) or a macroconch (CHANDLER & CALLOMON 2009). There is a great mor-

phological range between involute, unusually large-sized microconchs (Fig. 5.18) and involute macroconchs (Pl. 1, Fig. 6; Pl. 2, Fig. 5). Moreover, there are extremely small-sized but lapped microconchs, obviously representing adults (Figs. 5.16, 5.17). The typical narrow umbilicus of the morphospecies is developed in only a small proportion of the chronospecies *L. opalinum* (Figs. 5.15, 18; Pl. 1, Fig. 11; Pl. 2, Figs. 7, 8). Some of the specimens assigned to *Leioceras opalinum* from the Opalinum Zone of Fuentelsaz in Spain (GSSP for the base of the Aalenian; GOY & URETA 1987: pl. 1; GOY & URETA 1991: pl. 3) or from France (CONTINI 1969: pl. 6, figs. 1–3) are less involute than the holotype. Here we assigned ammonites with a slightly wider umbilicus as in the holotype of *L. opalinum* to the varieties *L. opalinum* var. *comata* or *L. opalinum* var. *buckmani*.

A. Types of the name-bearing morphospecies of the described varieties:

L. opalinum α var. *undatum* ex BUCKMAN, 1899 sp. [?m]

[HT: *Cylicoceras undatum* BUCKMAN, Suppl. p. 50, Suppl. pl. 5, figs. 5, 6; photograph in HOWARTH 2013, figs. 64.3a, b]

This is the coarsest-ribbed variety (Fig. 5.1), which is extremely rare in the *opalinum* Biohorizon. The coarsening of the ribbing in leioceratids leads to a weakening of the otherwise characteristic hair ribs. In extremely coarse-ribbed specimens, hair ribs are only discernible in some parts of the conch by using oblique illumination. The formation of coarse ribs obviously hampered the formation of hair ribs. HOWARTH (2013) interpreted the holotype of “*Cylicoceras*” *undatum* as a macroconchiate specimen. However, photographs of the holotype do not show any suture lines. Therefore, it can be a large-sized microconch as well. Such an early appearance of a “*Ludwigia*-like” whorl section and a similarly coarse ribbing are unknown from macroconchs of the Opalinum Subzone. Transitional forms to *Ludwigia* or the earliest species of that genus appear only towards the end of the Opalinum Zone (*L. praecursor* RIEBER, 1963 or extreme varieties of *Leioceras comptocostosum* CHANDLER & CALLOMON, 2009).

L. opalinum α var. *angulatum* ex MAUBEUGE, 1950 sp. [m]

[HT: *Pleydellia angulata* MAUBEUGE, p. 76, pl. 1 top]

This extremely rare variety (Fig. 5.2) is characterized by its large umbilicus and very widely spaced ribs.

L. opalinum α var. *buckmani* ex MAUBEUGE, 1947 sp. [m]

[HT: *Pleydellia buckmani* MAUBEUGE, p. 76, fig. 2 top]

“*Pleydellia*” *buckmani* is interpreted as a species linking the genera *Pleydellia* and *Leioceras* (OHMERT 1993; SCHULBERT 2001); its holotype comes from the uppermost Toarcian of Luxembourg. The specimens assigned to this variety (Fig. 5.13; Pl. 1, Figs. 7, 9, 10, 13; Pl. 2, Fig. 11) show fine, slightly bundled ribs towards the umbilical edge and a wider umbilicus than the holotype of *L. opalinum*. Our specimens are more slender than the holotype of *Pleydellia buckmani*.

L. opalinum α var. *costulatum* ex ZIETEN, 1830 sp. [?m]

[(unknown number of syntypes): *Ammonites costulatus* ZIETEN, 1830, p. 10, pl. 7, figs. 7a–c]

The herein illustrated example (Pl. 1, Fig. 15) differs from topotypes from the Upper Toarcian (Aalensis Subzone, Aalensis Zone) of Aalen-Wasseraalfingen only in its slightly more slender

whorl section (cf. ARP 2010, pl. 2, figs. 29–32). The whorl section of the syntype illustrated by ZIETEN (1830) is identical to that of our specimen.

L. opalinum α var. *leurum* ex BUCKMAN, 1890 sp. [m]

[LT: *Grammoceras leurum* BUCKMAN, 1890, Suppl. p. 138, pl. 33, figs. 8–10 (design. BUCKMAN 1902)]

This variety (Fig. 5.3; Pl. 1, Fig. 8; Pl. 2, Fig. 6) resembles *L. opalinum* var. *buckmani*, but the ribs in *L. opalinum* var. *leurum* are markedly wider spaced, especially in the nucleus, so that a bundling of the ribs at the umbilical wall is weakly developed or missing. The strongly proverse ventrolateral inclination of the ribs typical of *Leioceras* (Pl. 1, Fig. 8; Pl. 2, Fig. 6) differentiates most of our specimens from the lectotype of *Pleydellia leura*. Some specimens, however, are closer to the lectotype of the name-bearing variety (Fig. 5.3).

L. opalinum α var. *comatum* ex BUCKMAN, 1899 sp. [m]

[HT: *Pleydellia comata* BUCKMAN, Suppl. p. 137, pl. 10, figs. 11–13].

Pleydellia comata is the type species of *Pleydellia* BUCKMAN, 1899. Its umbilical width is transitional between that of the holotype of *L. opalinum* and *L. opalinum* var. *buckmani*. The whorl section of the holotype of *P. comata* is somewhat broader than in our specimens (Fig. 5.14; Pl. 1, Fig. 4; Pl. 2, Figs. 2, 3).

L. opalinum α var. *subcostosum* ex BUCKMAN, 1899 sp. [m]

[LT: *Lioceras subcostosum* BUCKMAN, Suppl. p. 37; Suppl. pl. 6, figs. 5–7 (design. CHANDLER & CALLOMON 2009)]

Since the taxon *L. costosum* (QUENSTEDT, 1886) is pre-occupied and thus, invalid (see Chapter 3.1.2.5.) we used the very similar *L. subcostosum* for naming varieties such as the examples illustrated on Figs. 5.10–5.11 and Pl. 1, Fig. 12 (CHANDLER & CALLOMON 2009).

L. opalinum α var. *tomum* ex BUCKMAN, 1904 sp. [m]

[HT: *Canavarella? toma* BUCKMAN, Suppl. p. 129, pl. 22, figs. 16–18].

This variety (Figs. 5.5–5.8; Pl. 1, Fig. 14) is characterized by its dense marked ribbing all across the flank that may occasionally fade away. It is close to the morphospecies *Pleydellia spathi* MAUBEUGE, 1947 and *P. falcifer* MAUBEUGE, 1950, but differs by its more slender, lanceolate whorl section. We also include specimens in this variety, which foreshadow the ribbing style of *L. bifidatum* (BUCKMAN) (Fig. 5.6).

L. opalinum α var. *gracile* ex BUCKMAN, 1899 sp. [m]

[HT: *Lioceras gracile* BUCKMAN, Suppl. p. 38, Suppl. pl. 6, figs. 11–13].

This very rare variety of the *opalinum* Biohorizon is characterized by a narrow umbilicus, a broad whorl section, prominent primaries and marked falcoid ventrolateral ribs (Fig. 5.4). The otherwise similar morphospecies *L. unicum* (BUCKMAN) is based on a macroconch.

L. opalinum α var. *arkelli* ex MAUBEUGE, 1950 sp. [m]

[HT *Pleydellia arkelli* MAUBEUGE, p. 380, pl. 10 bottom].

This rare but regularly occurring variant (Fig. 5.12) is extremely evolute. The morphospecies *Pleydellia misera* (BUCK-

MAN, 1902) is similarly evolute, but with a slightly lower whorl section.

***L. opalinum* α var. *arcuatum* ex BUCKMAN, 1901 sp. [m]** [HT: *Walkeria arcuata* BUCKMAN, Suppl. p. 139, pl. 32, figs. 11–12, Suppl. fig. 121].

A single specimen (Fig. 5.9) strongly resembles the ribbing style of “*Walkeria*” *arcuata*, otherwise characteristic for the Torulosum Subzone. It differs from the holotype of the latter by its more slender whorl section.

***Leioceras opalinum* α var. *subglabrum* ex BUCKMAN, 1902 sp. [M]** [HT: *Walkeria subglabra*, Suppl. p. 141; pl. 13, figs. 7–8].

This variety includes all macroconchiate leioceratids of the *opalinum* Biohorizon, with a single exception (see below). The diameter of adult specimens is up to 9 cm (Figs. 4.2, 4.4; Pl. 2, Figs. 4, 5, 10), only an exceptionally large specimen reaches 11.5 cm (Fig. 4.1). In adults, the fastigate venter becomes rounded at the end of the body chamber (Figs. 4.1a, 4.4a). The same characters can be observed in adult specimens of the morphospecies *L. subglabrum* from the top of the Bridport Sands at Burton Cliff, Dorset (coll. V.D.). Umbilical widths and whorl heights of macroconchs of the study area are variable (Figs. 4.2, 4.4). In juveniles, the umbilicus is relatively narrow (Fig. 4.1c; Pl. 1, Fig. 6) and widens in the adult stage in the last half whorl (Figs. 4.1b, 4.2b, 4.4b). In single specimens (Pl. 1, Fig. 5) the ventrolateral ribbing style is similarly pronounced as in the morphospecies *L. plicatum*.

***Leioceras opalinum* α var. *pseudoaalensis* ex MAUBEUGE, 1950 sp. [M]** [HT: *Pleydellia pseudoaalensis*, p. 378, pl. 9 top]

A single macroconchiate *Leioceras opalinum* α (Fig. 4.3) does not match with the variety *subglabrum*. It strongly recalls the morphology of *Pleydellia pseudoaalensis* originally described from the Upper Toarcian (Aalensis Zone, Torulosum Subzone) of Luxembourg. Its whorl section, involution and sculpture at the end of the phragmocone are also close to that of the morphospecies *L. renovatum* (BUCKMAN, 1899).

B. Variation in the chronospecies *Leioceras opalinum*

The macroconchs are rather uniform. They reach adult sizes of c. 9 cm. The sculpture consists only of fine hair-ribs. The umbilical width is slightly variable.

In the corresponding microconchs, variation is much greater. We found all transitions between almost smooth shells ornamented solely with fine hair-ribs, with a narrow umbilicus and a lanceolate whorl section (holotype of *L. opalinum*) to coarsely ribbed specimens with a broader whorl section and wide umbilicus (*L. opalinum* var. *undatum*). These extreme morphologies, however, are rare to very rare. Most microconchiate specimens are relatively involute and weakly sculptured (*L. opalinum*, *L. opalinum* var. *buckmani* bzw. var. *comatum*). BAYER (1972) studied the variation of *L. opalinum* based on material from the range area of the “Torulosum-Knollenlage” of

the former clay pit in Heiningen. Among the specimens he illustrated, there are remarkably small-sized but obviously adult microconchs less than 10 mm in diameter (cf. Figs. 5.16, 5.17).

4.1.3.2. *dilucidum* Biohorizon (Dilucidum-Schichten)

Leioceratids of the *dilucidum* Biohorizon are assigned to the chronospecies *Leioceras opalinum* as well. Our studied sample is too small to assess whether the variation in the microconchs and the adult size of the macroconchs has significantly changed. A single fragment of an adult macroconch (Pl. 3, Figs. 9a–b) points to an estimated maximum diameter of c. 11–12 cm. Compared to the *opalinum* Biohorizon, we noticed a lower number of *Pleydellia*-like varieties and more involute microconchs close to the holotype of *L. opalinum*. Therefore, we distinguished between an α -morph of *L. opalinum* for the specimens of the *opalinum* Biohorizon and a β -morph for those of the *dilucidum* Biohorizon. The varieties of the *dilucidum* Biohorizon are the same as those occurring in the *opalinum* Biohorizon (see above).

4.1.3.3. ?*opaliniforme* Biohorizon (Lucinenbank)

We determined the few poorly preserved specimens of the Lucinenbank as *L. ex gr. opaliniforme* var. *opalinum* (Fig. 7.1) and *L. ex gr. opaliniforme* (Fig. 7.2), respectively, taking into account their adult diameters of more than 10 cm.

4.1.3.4. ?*opaliniforme* Biohorizon (Level of the Pentacrinitenplatten)

We recovered two well determinable ammonites and several body chambers of leioceratids with a diameter of at maximum 12 cm from this part of the section. Here we illustrate examples of *L. ex gr. opaliniforme* (Pl. 4, Figs. 1, 3).

4.1.3.5. *opaliniforme* Biohorizon (Opaliniforme-Schichten [= K 10–K 13 in KOBLER 1972])

***Leioceras opaliniforme* (BUCKMAN, 1899)** [LT, designated herein: *Cypholoceras opaliniforme* BUCKMAN, 1899, Suppl. p. 55; pl. 13, figs. 1–3].

We concur with OHMERT (1993) and assigned the body chamber fragments from the claystones (Pl. 7, Figs. 1–2; Pl. 8, Figs. 2–3, Pl. 9, Fig. 7) to *L. opaliniforme* (BUCKMAN). Juvenile and adult specimens are similarly common. *L. opaliniforme* differs from the stratigraphically younger *L. hansrieberi* by its on average smaller adult size ranging between 13.0 cm and 15.5 cm and its flanks mostly lacking the undulating bulges at the transition phragmocone/body chamber (DIETZE & SCHWEIGERT 2018). Exceptionally, such bulges already appear in *L. opaliniforme* (Pl. 8, Fig. 1). These are transitional forms linking *L. opaliniforme* and *L. hansrieberi*. The venter of the body chamber of adult specimens is rounded (Pl. 7, Figs. 1b, 2b), whereas it is still fastigate in juveniles (Pl. 8, Figs. 2a, 3b). The aperture swings

slightly forward at mid-flank (Pl. 7, Fig. 2a; Pl. 9, Fig. 1b). The sculpture of the innermost whorls is variable (Pl. 9, Figs. 3–5) but gets lost during further growth. The small, evolute ammonite shown on Pl. 9, Fig. 6 most likely is a microconch. Microconchs are extremely rare in the claystones.

In contrast, in the “Opalinusknohlen” microconchs predominate, whereas fragments of body chambers (Pl. 5, Fig. 10) or complete macroconchs are exceptional finds. Only a single “Opalinusknohle” with a diameter of c. 25 cm yielded numerous compressed macroconchs up to a diameter of 15.5 cm (Pl. 5, Fig. 10). Besides the illustrated ammonites of the individual “Opalinusknohlen” (each labelled with roman numerals) additional fossils were deposited in the SMNS collection.

Most macroconchs are almost smooth-shelled and show only fine hair-ribs. Their umbilicus is relatively wide. Their morphology fits very well with that of *L. opaliniforme* (Pl. 5, Figs. 10; Pl. 7, Figs. 1, 2; Pl. 9, Figs. 1, 7). Juveniles or innermost whorls still lacking the rounded venter of adults are also included in *L. opaliniforme* (Pl. 8, Figs. 2, 3, Pl. 9, Figs. 2–5).

L. opaliniforme is the earliest described species coming definitely from this horizon; hence, we took that name for naming the chronospecies.

A. Types of the name-bearing morphospecies of the described varieties

L. opaliniforme var. *hansrieberi* ex DIETZE & SCHWEIGERT, 2018 sp. [M]

The morphospecies *L. hansrieberi* exhibits a rounded venter in the body chambers of adults and a stage showing broad, wavy bulges on the flanks (Pl. 7, Fig. 3; Pl. 8, Fig. 1). *L. lineatum* is very close, but differs by a less rounded venter and weaker development of bulges. Alternatively, the juvenile specimen of Pl. 8, Fig. 1 could be included in the variety *lineatum* as well. DIETZE & SCHWEIGERT (2018) introduced *L. hansrieberi* as a new chronospecies, since no other *Leioceras* species had been previously described from its type horizon.

L. opaliniforme var. *tyrrhenum* ex KUHN, 1934 sp. [M] [3 syntypes: *Leioceras tyrrhenum* KUHN, 1934, p. 25; fig. 6; pl. 2, fig. 3]

The macroconchs from an “Opalinusknohle” (Pl. 6, Fig. 2a, Figs. 11d–f [= lateral views of the same “Opalinusknohle”]) are assigned to this variety. The similar morphospecies *L. plectile* (BUCKMAN, 1899) and *L. plicatellum* (BUCKMAN, 1899) differ by their markedly elongated thickenings of the ribs at mid-flank.

L. opaliniforme var. *partitum* ex BUCKMAN, 1899 sp. [m] [three syntypes: *Lioceras partitum* BUCKMAN, 1899, Suppl. p. 39, pl. 13, fig. 11; pl. 14, figs. 3, 4 [= LT designated herein], Suppl. pl. 9, figs. 4–6].

BUCKMAN (1899) included both microconchs and macroconchs in *L. partitum*. Here we select a microconchiate specimen (BUCKMAN 1899: pl. 14, figs. 3, 4) as the lectotype.

Most of the microconchiate leioceratids of the *opaliniforme* Biohorizon (Pl. 5, Figs. 2a, 4, 5, 7–9, 12b; Pl. 6, Figs. 1, 2b, 3–5, 7, 9, 10, 11a, c) exhibit a very typical ribbing style. The hair-ribs are bundled at their bases and form more or less pronounced falcoid ribs, which weaken towards the venter. *L. undulatum* (BUCKMAN) is rather similar but differs by its broader whorl section.

L. opaliniforme var. *opalinum* ex REINECKE, 1818 sp. [m]

Some of our specimens (e.g., Pl. 5, Fig. 1) are indistinguishable from the type species of *Leioceras*.

L. opaliniforme var. *comatum* ex BUCKMAN, 1899 sp. [m]

In the *opaliniforme* Biohorizon, the variety *comatum* (Pl. 5, Figs. 2b, c, 11; Pl. 6, Fig. 12) is still present. It differs from the holotype of *L. opalinum* by its wider umbilicus.

L. opaliniforme var. *subcostosum* ex BUCKMAN, 1899 sp. [m]

Occasionally, the relatively coarsely ribbed variety *L. opaliniforme* var. *subcostosum* occurs (Pl. 5, Fig. 12a; Pl. 6, Figs. 6, 13–14).

B. Variation in the chronospecies *Leioceras opaliniforme*

Adult macroconchs of the *opaliniforme* Biohorizon are quite uniform. Their maximum diameters are c. 13–15.5 cm. Apart from hair-ribs, the flanks are smooth. Only few specimens show rudimentary slender lateral bulges thus anticipating the subsequent chronospecies *L. hansrieberi*.

The corresponding microconchs are similar to *L. opaliniforme* var. *partitum* showing more or less pronounced bundled ribs on the flanks. The conch morphology is markedly more evolute than in most microconchs of the *opalinum* and *dilucidum* biohorizons. They are accompanied by smooth-shelled specimens resembling *L. opalinum* s. str. and the stronger ribbed variety *subcostosum*.

4.1.3.6. *hansrieberi* Biohorizon (Wasserfallschichten and base of Op 2)

Leioceras hansrieberi (DIETZE & SCHWEIGERT, 2018) [HT: DIETZE & SCHWEIGERT 2018: 32, figs. 3a, b].

The c. 10 m thick interval extending from c. 2 m below the base of the waterfall up to c. 2 m above the top of the Wasserfallschichten yields abundant *Leioceras hansrieberi* DIETZE & SCHWEIGERT (for details of this taxon see DIETZE & SCHWEIGERT 2018). Up to 4.9 m below the top of the Wasserfallschichten the leioceratids are preserved with white aragonitic shells (Pls. 10–13), further up they show brownish calcitic shells (Pls. 14–17). Initially, the white-shelled macroconchs are relatively large and show maximum diameters of c. 20 cm (Pl. 12, Fig. 2; Pl. 13, Fig. 1). Simultaneously with the change of the shell mineralogy, which is related to an increased sand content of the claystones (ANDALIB 1970), they become smaller-sized (Pl. 14, Fig. 1; Pl. 15, Figs. 1, 2; Pl. 16, Fig. 1). However, in the top of the *hansrieberi* Biohorizon the shells reach again diameters of significantly more than 20 cm (Pl. 17, Fig. 1). Obviously living conditions got worse when sand was deposited, but then the conditions ameliorated again.

A. Types of the name-bearing morphospecies of the described varieties

***L. hansrieberi* var. *partitum* ex BUCKMAN, 1899 sp. [m]**

We assign the microconchs from the lithified claystone (Pl. 14, Figs. 2, 4) and calcareous nodules (Pl. 14, Fig. 3) and a few specimens from the 'Opalinusknohlen' (Pl. 10, Figs. 2, 3, 5, 7d, e) to *L. hansrieberi* var. *partitum*.

***L. hansrieberi* var. *subcostosum* ex BUCKMAN, 1899 sp. [m]**

This variety is relatively common in the *hansrieberi* Biohorizon (Pl. 10, Figs. 1, 4, 6, 7a, b). The *hansrieberi* Biohorizon is the type horizon of the invalid species *L. costosum* (QUENSTEDT) (see Chapter 3.1.1.5). The morphospecies *L. subcostosum* und *L. costosum* are nearly identical (CHANDLER & CALLOMON 2009).

B. Variation of the chronospecies *Leioceras hansrieberi*

Macroconchs of the chronospecies *L. hansrieberi* are the biggest leioceratids. Their adult diameters reach 24 cm, exceptionally even 30 cm (KOBLE 1967, 1972). The variation in the macroconchs is very small. They subtly differ in the relief of the wavy ribs at the beginning of the body chamber. In adults, the venter of the body chamber varies between broadly-rounded and rounded-fastigate.

Microconchs vary between weakly ribbed forms (*L. hansrieberi* var. *partitum*) and coarsely ribbed morphologies (*L. hansrieberi* var. *subcostosum*).

4.1.3.7. *bifidatum/rieberi* Biohorizon (Bifidatumbank [formerly Costosumbank])

***Leioceras bifidatum* (BUCKMAN, 1899) [M] [2 ST: *Leioceras bifidatum* BUCKMAN, 1899, p. 38, pl. 7, figs. 1–6].**

L. bifidatum (Pl. 19, Fig. 4) is characterized by its flexicostate, bundled ribs and a fastigate venter. *L. thompsoni* (BUCKMAN, 1899) lies within the variation of the morphospecies *L. bifidatum*. The use of the taxon *L. bifidatum* has position precedence (ICZN 1999, Art. 69A.10).

A. Types of the name-bearing morphospecies of the described varieties

***L. bifidatum* var. *rieberi* ex GÉCZY, 1967 sp. [M] [HT: *Leioceras comptum rieberi* GÉCZY 1967, p. 169, pl. 27, fig. 1; text-fig. 170].**

Within the populations of the *bifidatum/rieberi* Biohorizon, large-sized, moderately evolute leioceratids (Pl. 18, Figs. 1a, b; Pl. 19, Figs. 1a, b) with a rounded venter of the body chamber are assigned to *L. bifidatum* var. *rieberi*. Some of them still show the wavy bulges at the beginning of the body chamber (Pl. 19, Figs. 2a, b), resembling the elder *L. hansrieberi*. An extraordinarily evolute specimen is anticipating the younger chronospecies *L. evolutum*, apart of its much bigger size. It is determined as *L. bifidatum* var. aff. *rieberi* (Pl. 18, Figs. 2a, b).

***L. bifidatum* var. *spathi* ex GÉCZY, 1967 sp. [M] [HT: GÉCZY (1967), p. 165, pl. 36, fig. 2, pl. 64, fig. 77; text-fig. 165].**

L. spathi (Pl. 19, Fig. 5) is a rare, almost unsculptured involute variety.

***L. bifidatum* var. cf. *crassicosum* ex RIEBER, 1963 sp. [M] [HT: *Leioceras crassicosum*, p. 37, pl. 1, figs. 10, 11]**

The specimens assigned to *L. bifidatum* var. cf. *crassicosum* (Pl. 18, Figs. 6, 8–10) differ from the holotype and numerous topotypes of *L. crassicosum* by their slightly narrower umbilicus, a greater whorl section in comparable growth stages and a smaller adult size.

***L. bifidatum* var. *uncinatum* ex BUCKMAN, 1899 sp. [M] [unknown number of syntypes, *Leioceras uncinatum* BUCKMAN, 1899, Suppl. p. 36, Suppl. pl. 5, figs. 7, 8 [= LT designated herein], 9–11 and synonymy list]**

Two compressed specimens (e.g., Pl. 18, Fig. 7) correspond well to *L. uncinatum* from the succeeding *uncinatum* Biohorizon.

***L. bifidatum* var. *plicatellum* ex BUCKMAN, 1899 sp. [M] [HT: *Leioceras plicatellum* BUCKMAN, 1899, Suppl. p. 38, Suppl. pl. 11, figs. 7–9]**

L. bifidatum var. *plicatellum* (Pl. 19, Figs. 3, 6) is characterized by its weak ribbing, which is only more pronounced by bundles at mid-flank. This ribbing weakens on the body chamber. *L. plectile* (BUCKMAN, 1899) and *L. tyrrhenum* (RENZ, 1934) are similar, but have other whorl sections.

The taxonomic treatment of the microconchiate leioceratids of the *bifidatum/rieberi* Biohorizon – and also the *uncinatum* and *evolutum* biohorizons – is problematic. They show a combination of characters ranging from almost smooth to coarsely ribbed, involute and evolute conchs and slender as well as broad whorl sections. In contrast to the *opalinum* Biohorizon, there are less described morphospecies to be used for the naming of the varieties. We were guided by RIEBER (1963) and CONTINI (1997), who solved these problems by lumping the numerous transitional morphologies into only a few nominal species.

***L. bifidatum* var. *partitum* ex BUCKMAN, 1899 sp. [m]**

Microconchiate leioceratids from the lower part of the Bifidatumbank (bed BB-1) are characterized by their slender whorl section and falcate ribs showing swellings just below mid-flank. The few recovered specimens are remarkably uniform and fit well with the group of *L. bifidatum* (cf. BUCKMAN 1899, pl. 7, figs. 4–6). Since we interpret *L. bifidatum* as a macroconch, the microconchs are included in the variety *partitum* (Pl. 18, Figs. 3–5). In bed BB-2, however, *L. bifidatum* var. *partitum* (Pl. 20, Figs. 9, 10) is only a subordinate variety.

***L. bifidatum* var. aff. *subcostosum* ex BUCKMAN, 1899 sp. [m]**

Specimens assigned to *L. bifidatum* var. aff. *subcostosum* (Pl. 20, Figs. 13–15a) differ from the variety *subcostosum* by a weakening of the ribbing on the body chamber.

***L. bifidatum* var. *paucicostatum* ex RIEBER, 1963 sp. [m]**
[HT: *Leioceras paucicostatum* RIEBER, 1963, p. 35, pl. 2, figs. 4, 5]

These extremely coarsely ribbed microconchs (Pl. 20, Fig. 16) are in a very marginal position within the generally more weakly sculptured leioceratids of the *bifidatum/rieberi* Biohorizon.

***L. bifidatum* var. *striatum* ex BUCKMAN, 1899 sp. [m]**
[several syntypes: *Lioceras striatum* BUCKMAN, 1899, p. 42, [1888]: pl. 13, figs. 6, 12 [the HT according to RIEBER (1963)], Suppl. pl. 10, fig. 10 and synonymy]

In bed BB-2, there is a range between delicately ribbed specimens (Pl. 20, Figs. 1–3) to slightly stronger ribbed forms, in which the fine ribs are bundled on the flank forming somewhat elevated ribs (Pl. 20, Figs. 4–7). Several finely ribbed microconchs (Pl. 20, Figs. 8, 11, 12) are assigned to *L. bifidatum* aff. *striatum*. For these ammonites no morphospecies has been introduced. In the literature, they have been determined as *L. “comptum”* (URETA GIL 1983: pl. 3, figs. 10, 11), *L. paucicostatum* (SEYED-EMAMI et al. 2005: figs. 7A, C), or “*Ludwigia costosa*” (HOFFMANN 1913: pl. 2, figs. 10–11, 13, 15).

B. Variation in the chronospecies *Leioceras bifidatum*

Macroconchs may reach up to 10 cm in diameter, but most of them are smaller. The most common varieties are relatively smooth forms with an intermediate umbilical width. They are accompanied by coarsely ribbed specimens, which are significantly small-sized.

Most of the microconchs are weakly sculptured. Only a small portion of our specimens exhibits a coarser ribbing. In general, the whorl section is relatively broad and the venter is broadly fastigate.

4.1.3.8. *uncinatum* Biohorizon (Top Zopflatten [ZoP 5–6])

***Leioceras uncinatum* (BUCKMAN, 1899) [M]** [unknown number of syntypes, *Lioceras uncinatum* BUCKMAN, 1899, Suppl. p. 36, Suppl. pl. 5, figs. 7, 8 [=LT designated herein], 9–11 and synonymy]

Due to nomenclatorial stability, here we designate the specimen illustrated by BUCKMAN (1899: pl. 5, figs. 7, 8) from the Scissum Bed of Burton Bradstock as the lectotype. Our own specimens (Pl. 21, Figs. 1–4) vary a little in the strength of the ribbing, but fit very well with this lectotype. *L. crassicosatum* RIEBER differs from *L. uncinatum* by a wider umbilicus, a lower whorl height, a smaller adult size, and a more rounded body chamber. *L. unum* (BUCKMAN, 1899) and *L. gracile* (BUCKMAN, 1899) are more involute than typical *L. uncinatum*, but are within the variation of this species (see CONTINI 1969). *L. uncinatum* (as chronospecies as described here) has nomenclatorial priority over all other leioceratids described in BUCKMAN (1899), hence also over *L. unum* and *L. gracile*.

A. Types of the name-bearing morphospecies of the described varieties

***L. uncinatum* var. *plectile* ex BUCKMAN, 1899 sp. [M]**
[Suppl., p. 39; Suppl. pl. 9, figs. 10–12a]

This variety (Pl. 22, Fig. 5) is transitional between coarsely and finely ribbed macroconchs of the *uncinatum* Biohorizon. *L. plicatellum* is very close to *L. plectile*, but exhibits a more slender whorl section.

***L. uncinatum* var. *stephanovi* ex SAPUNOV, 1970 sp. [M]**
[HT: *Cylicoceras stephanovi*, p. 68, pl. 2, figs. 1a–c]

Ammonites assigned to this variety (Pl. 21, Fig. 5; Pl. 22, Fig. 6) resemble leioceratids of the *crassicosatum* Biohorizon. However, adult macroconchs of the *crassicosatum* Biohorizon are smaller and have a more slender whorl section. *L. rieberi* GÉCZY differs from the variety *stephanovi* by its smooth flanks.

***L. uncinatum* var. *plicatellum* ex BUCKMAN, 1899 sp. [M]**

To this variety we assign relatively weakly ribbed specimens (Pl. 22, Figs. 3, 4, 7, 8a, 8e) showing a narrow umbilicus, slender whorl section and a fastigate venter.

***L. uncinatum* var. *bifidatum* ex BUCKMAN, 1899 sp. [M]**

Despite of their slightly wider umbilicus, we included the ammonites of Pl. 22, Figs. 1, 2 in the variety *L. uncinatum* var. *bifidatum*.

***L. uncinatum* var. *partitum* ex BUCKMAN, 1899 sp. [m]**

Microconchs with distantly bundled ribs (Pl. 23, Figs. 10–12, 15) are determined as *L. uncinatum* var. *partitum*. The specimen illustrated on Pl. 23, Fig. 11 is transitional between the varieties *subcostosum* and *partitum*. The specimen of Pl. 23, Fig. 14 exhibits a remarkably wide umbilicus, but considering its ribbing style it is included in the variety *partitum* as well.

***L. uncinatum* var. *subcostosum* ex BUCKMAN, 1899 sp. [m]**

The variety *L. uncinatum* var. *subcostosum* (Pl. 22, Figs. 8c, d; Pl. 23, Figs. 3, 4, 9, 13, 18) is relatively common in the *uncinatum* Biohorizon.

***L. uncinatum* var. *striatum* ex BUCKMAN, 1899 sp. [m]**

In this variety we include weakly sculptured microconchs, which develop a thickening of the ribs at mid-flank at various ontogenetic stages (Pl. 22, Fig. 8b; Pl. 23, Figs. 16–17, 19–23).

***L. uncinatum* var. *paucicostatum* ex RIEBER, 1963 sp. [m]**

Like in the *crassicosatum* Biohorizon of the western Swabian Alb (RIEBER 1963), the coarsely ribbed microconchs are pretty variable, especially with respect to their final size (Pl. 23, Figs. 1–2, 5–8).

B. Variation in the chronospecies *Leioceras uncinatum*

The macroconchs from the area described in this paper are relatively large-sized with respect to the leioceratids of the Bifidatum Subzone and can reach up to 13 cm in diameter. Three main morphologies can be differentiated: (1) coarsely ribbed forms with a fastigate venter even in the body chamber, (2) forms with a rounded venter of the body chamber resembling specimens from the *crassicos-tatum* Biohorizon of the western Swabian Alb (RIEBER 1963), except of their larger adult sizes, and (3) relatively weakly ribbed forms in the style of *L. bifidatum*.

The microconchs are extremely variable concerning ribbing, coiling, and conch width. Even the adult size ranges between slightly more than 2 cm and exceeding 6 cm.

4.1.3.9. *evolutum* Biohorizon (Wilflingen-Bank [formerly Comptumbank])

Leioceras evolutum CONTINI, 1969 [HT: *Leioceras* (*Cypholioceras*) *comptum* (REIN.) *evolutum* morphotype *subcostate*, p. 19, pl. 9, figs. 1a, b].

From the “Comptum” Subzone [= Bifidatum Subzone] of Franche-Comté CONTINI (1969) reported very evolute leioceratids up to 8 cm in diameter. The broad, fastigate venter of the phragmocone becomes rounded on the body chamber. With respect to their variable ribbing, he distinguished between the morphological variants *striate*, *subcostate* and *costate*. Here we use them in the same sense. Specimens showing a coarse ribbing in all stages have been assigned to *L. (Cylicoceras) crassicos-tatum* RIEBER (CONTINI 1969: 4). This species is remarkably common at Amaurandes du Bas. *Leioceras evertens* (BUCKMAN, 1899) is not an appropriate index species, since after BUCKMAN (1899: suppl. pl. 1, figs. 10–12) its type horizon at Mapperton (Dorset) is unclear. Either it comes from the Murchisonae Zone or from the Scissum Zone of southern England (= Bifidatum Subzone). The chronospecies of this time slice should not be named after a species with an unknown type horizon, possibly coming from the Upper Aalenian.

A. Types of the name-bearing morphospecies of the described varieties

L. evolutum var. *striate* sensu CONTINI, 1969 [M] [pp. 19, 20; pl. 8, fig. 9; MAUBEUGE 1955, pl. 3, fig. 3; pl. 5, fig. 2]

This variety is characterized by its fine, relatively dense ribbing (Pl. 24, Figs. 6–8; Pl. 25, Figs. 2, 3b, c, 4–5; Pl. 26, Figs. 7–12).

L. evolutum var. *subcostate* sensu CONTINI, 1969 [M] [pp. 19, 20; pl. 8, fig. 10; pl. 9, figs. 1a, b]

Typical are wider spaced, stronger primaries; the body chamber can become smooth (Pl. 24, Fig. 5; Pl. 26, Figs. 4–6).

L. evolutum var. *costate* sensu CONTINI, 1969 [M] [pp. 19, 20, pl. 9, figs. 2, 3; BUCKMAN 1899, pl. 7, figs. 10–12; pl. 11, figs. 10–12]

Continuously sculptured, moderately strongly ribbed specimens represent the variant *costate* sensu CONTINI (Pl. 24, Fig. 4; Pl. 25, Figs. 1, 3a; Pl. 26, Figs. 1–3). The ammonite illustrated on Pl. 25, Fig. 1 still shows a slightly fastigate, less rounded venter.

L. evolutum var. *crassicos-tatum* ex RIEBER, 1963 sp. [M]

We partly follow CONTINI (1969), who has determined ammonites with a strong ribbing up to the aperture as *L. crassicos-tatum*. The holotype and the specimens illustrated by RIEBER (1963) as topotypes and chorotypes are slightly more involute than our material. Therefore, here we use this taxon name only to describe a variant of the chronospecies *L. evolutum* (Pl. 24, Figs. 2, 3).

L. evolutum var. *comptocostosum* ex CHANDLER & CALLOMON, 2009 sp. [M] [HT: p. 120, pl. 1, figs. 1a, b]

A single specimen (Pl. 24, Fig. 1) exhibits a remarkably broad whorl section and is ornamented with thick, widely spaced ribs. It compares favourably with specimens from Southern England that are described as “biospecies” *L. comptocostosum* (CHANDLER & CALLOMON 2009, pl. 1, fig. 1 [HT], pl. 2, fig. 1).

L. evolutum var. *paucicostatum* ex RIEBER, 1963 sp. [m]

Following RIEBER (1963), who identified the microconchiate leioceratids from the slightly older *crassicos-tatum* Biohorizon of the western Swabian Alb as *L. paucicostatum* and *L. striatum*, the coarser-ribbed specimens are here termed as variant *paucicostatum*, and finely ribbed to almost smooth-shelled ones are assigned to the variant *striatum*. The whorl sections of microconchiate leioceratids of the *evolutum* Biohorizon are broader than those of the *crassicos-tatum* Biohorizon. Microconchs are almost restricted to concretions. Some of them are full of microconchiate leioceratids and bivalves and shell fragments. The ammonites illustrated on Pl. 25, Figs. 6a, 7, 8, 13–18, 23a are determined as *L. evolutum* var. *paucicostatum*, whereas those of Pl. 25, Figs. 16, 18 are transitional to *L. evolutum* var. *striatum*.

L. evolutum var. *striatum* ex BUCKMAN, 1899 sp. [m] [syntypes see above]

The microconchs illustrated on Pl. 25, Figs. 9–12, 19–22, 23b–25 represent *L. evolutum* var. *striatum*. The specimens on Pl. 25, Figs. 19–20 and 22 are transitional to *L. evolutum* var. *paucicostatum*.

B. Variation within the chronospecies *Leioceras evolutum*

Adult macroconchiate specimens of the chronospecies *L. evolutum* are relatively uniform, with a diameter of c. 8 cm, a rounded venter on the body chamber, a depressed whorl section and an evolute coiling. Most specimens exhibit a weak ornamentation; only a few ones are stronger or coarse-ribbed. In the microconchs, the section of the venter on the body chamber is usually broad fastigate,

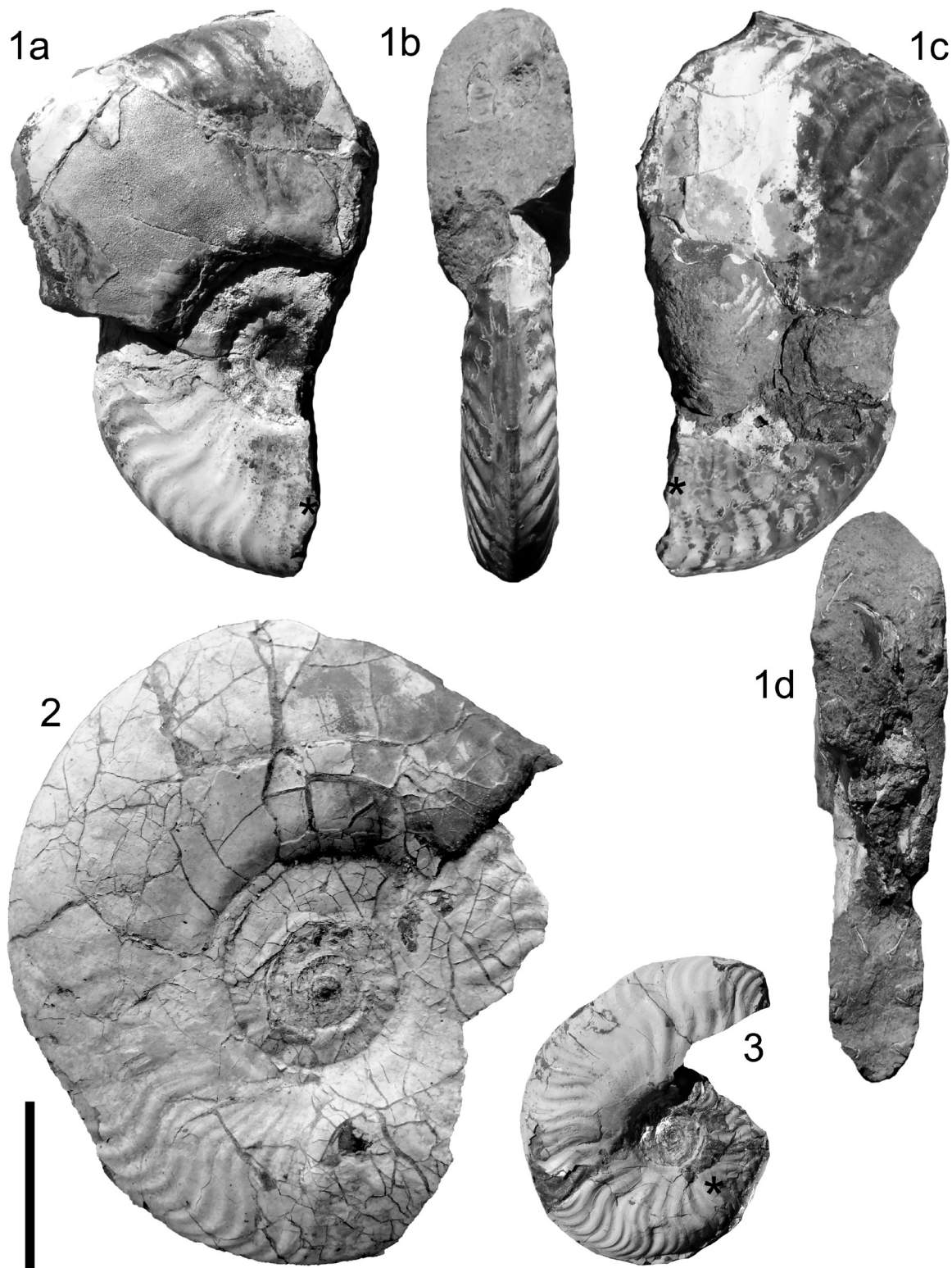


Fig. 13. (1, 2): *Canavarella fasciata* (BUCKMAN) [M], (1) Heiningen, Teufelsloch Member, range area of the Torulosum concretion layer, *opalinum* Biohorizon, SMNS 70608/43, (2) Aichelberg slope of the motorway A8, Zillhausen Member, base of the Wasserfall-schichten, *hansrieberi* Biohorizon, SMNS 70608/44. (3): *Canavarella fasciata* (BUCKMAN) [m], Teufelsklingenbach gorge, Teufelsloch Member, Opaliniforme-Schichten, *opaliniforme* Biohorizon, SMNS 70608/45. (1–3) Opalinuston Formation; Lower Aalenian, Opalinum Zone, Opalinum Subzone. Ammonites slightly reduced in size. Scale bar equals 30 mm.

occasionally rounded. The ribbing varies from almost smooth to coarse. Typical are, as in the macroconchs, a relatively broad whorl section and a large umbilicus.

**4.2. Genus *Canavarella* BUCKMAN, 1904
(Family Graphoceratidae BUCKMAN, 1905;
Subfamily Leioceratinae SPATH, 1936)**

Type species: *Canavarella belophora* BUCKMAN, 1904.

Remarks: Here we follow HOWARTH (2013), who kept the genus *Canavarella* separate from the genus *Leioceras* with respect to its remarkable falconid ribbing. We assign the specimens from the Opalinum Subzone to *C. fasciata* (BUCKMAN, 1899) (Figs. 13.1–13.3).

**4.3. Genus *Ancolloceras* BUCKMAN, 1899
(Family Graphoceratidae BUCKMAN, 1905;
Subfamily Leioceratinae SPATH, 1936)**

Type species: *Ancolloceras substriatum* BUCKMAN, 1899.

Remarks: The recorded specimens of *Ancolloceras opalinoides* (Figs. 12.1–12.3, 12.5–12.7, 12.9–12.12, 12.14–12.16) from bed AF-3 are illustrated here to demonstrate the beginning of the Upper Aalenian (Murchisonae Zone, Haugi Subzone).

Our records of *Ancolloceras opalinoides* from the Teufelsloch gorge comprise weakly ribbed to markedly ribbed macroconchs (Figs. 12.1–12.3, 12.5–12.7, 12.10, 12.11) as well as numerous evolute and smaller-sized microconchs (Figs. 12.12, 12.14–12.16). Here we follow RIEBER (1963) and CONTINI (1969), who included all varieties of *Leioceras acutum* (HORN, 1909, pre-occupied) in *A. opalinoides*.

Specimens tentatively determined as ?*Leioceras* sp. (macroconch: Fig. 12.4; microconchs: Fig. 12.8, 12.13) share characteristics of the genera *Ancolloceras* and *Leioceras*. The exact taxonomic assignment of these ammonites is beyond the scope of this work.

**4.4. Genus *Pleurolytoceras* HYATT, 1900
(Family Lytoceratidae NEUMAYR, 1875; Subfamily
Alocolytoceratinae SPATH, 1927)**

Type species: *Ammonites hircinus* SCHLOTHEIM, 1820.

Remarks: HOFFMANN (2015) considered the genus *Pachylotoceras* BUCKMAN, 1905 (type species: *Ammonites torulosus* ZIETEN, 1830) as a junior synonym of *Pleurolytoceras*. This is evident, since *P. hircinus* is a direct ancestor of *P. torulosum* (SCHULBERT 2001). *P. torulosum* (Pl. 1, Figs. 1, 3; Pl. 2, Fig. 1), *P. taeniatum* (POMPECKJ) (POMPECKJ 1897, pl. 12, figs. 5–7) and *P. penicillatum* (QUENSTEDT) are common in the opalinum Biohorizon. *P. dilucidum* (OPPEL) is a very common species especially of the dilucidum Biohorizon (Pl. 3, Figs. 14–17), but it appears already in the opalinum Biohorizon and ranges at least up to the opaliniforme Biohorizon (Pl. 8, Figs. 4, 5). In the latter, rare body chamber fragments of *P. penicillatum* occur. An indeter-

minable fragment of a *Pleurolytoceras* was even found in the bifidatum/rieberi Biohorizon (SMNS 70608/209).

**4.5. Genus *Hypophylloceras* SALFELD, 1924
(Family Phylloceratidae ZITTEL, 1884; Subfamily
Calliphylloceratinae SPATH, 1927)**

Type species: *Phylloceras ononense* STANTON, 1896.

Remarks: We concur with HOWARTH (2020), who treats the genus *Calliphylloceras* SPATH, 1927 as a junior synonym of *Hypophylloceras* SALFELD, 1924. The genus *Holcophylloceras* is more evolute and shows a more sigmoidal ribbing style than the genus *Hypophylloceras* (JOLY 1990; HOWARTH 2020). A one centimetre-sized nucleus from the opalinum Biohorizon of Heiningen (coll. W. DANGELMAIER) can only be determined as *Hypophylloceras* sp.

**4.6. Genus *Tmetoceras* BUCKMAN, 1892
(Family Hildoceratidae HYATT, 1867; Subfamily
Tmetoceratinae SPATH, 1936)**

Type species: *Ammonites scissus* BENECKE, 1865.

Remarks: We have only one single, strongly compressed specimen of *T. scissum* (Pl. 15, Fig. 3) from the hansrieberi Biohorizon of the Teufelsloch gorge. RIEBER (1963) mentioned the co-occurrence of *Tmetoceras scissum*, *Leioceras opalinum* and *Scaphotrigonia navis* in the Teufelsloch gorge. KOBLER (1967) clarified that the *Tmetoceras* specimen derived from the basal Wasserfallschichten corresponds to the hansrieberi Biohorizon.

**4.7. Genus *Bredya* BUCKMAN, 1910
(Family Hammatoceratidae BUCKMAN, 1887;
Subfamily Hammatoceratinae BUCKMAN, 1887)**

Type species: *Burtonia crassornata* BUCKMAN, 1910 (= *Ammonites subinsignis* OPPEL, 1856).

Remarks: SCHWEIGERT (1996) pointed out that the lectotype of *B. subinsignis* (illustrated in RENZ 1925: pl. 1, fig. 5 and HOWARTH 2013: figs. 72.3a, b) from Gomaringen near Tübingen designated by SENIOR (1977) originates from the Aalensis Zone (Upper Toarcian), which extends in that area into the basal Opalinuston Formation. Two specimens from Heiningen (Figs. 5.19, 5.20) and another newly collected one from the Pliensbach creek (Pl. 3, Fig. 13) are recorded from the opalinum and dilucidum biohorizons of the Opalinum Subzone, respectively. A perfectly preserved specimen of *B. subinsignis* was found in the opaliniforme Biohorizon temporarily exposed at the construction of the motorway A8 along the Aichelberg slope (Fig. 14.1).

5. Biostratigraphy

The seven ammonite biohorizons recognized in the Opalinuston Formation of the study area belong to the Opalinum Zone (Lower Aalenian).



Fig. 14. (1): *Bredya subinsignis* (OPPEL) [M], SMNS 70608/46, Aichelberg slope of the motorway A8, Opalinuston Formation, Zillhausen Member, c. 20 m below Wasserfallschichten [= Opaliniforme-Schichten]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites slightly reduced in size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

Subst.	Zone	Subzone	Biohorizons	Occurrences in SW Germany
Upper Aalenian (pars)	Murchisonae	Haugi	<i>opalinoides</i> yet to be worked out ⁴	Swabian Alb, Wutach area (RIEBER 1963) Aichelberg area [DIETL 2013; here], Geisingen [DIETZE et al. 2014]
Lower Aalenian	Opalinum	Bifidatum [ex Comptum] ¹	<i>evolutum</i> <i>crassicostatum</i> ^{2,3} <i>uncinatum</i> <i>bifidatum/rieberi</i>	Aichelberg area, ?eastern part of W Swabian Alb Swabian Alb, Wutach [RIEBER 1963], N Franconian Alb [DORN 1935] Aichelberg area Aichelberg area
		Opalinum	<i>hansrieberi</i> <i>opaliniforme</i> <i>dilucidum</i> <i>opalinum</i>	Swabian Alb [OHMERT 1993, DIETZE & SCHWEIGERT 2018] Swabian Alb [OHMERT 1993] Swabian Alb, N Franconian Alb [SCHULBERT 2001] Swabian Alb, Wittnau [OHMERT 1993; non SCHULBERT 2001]

Fig. 15. Biohorizons of the Opalinum Zone and the Murchisonae Zone, Haugi Subzone in the Middle Jurassic of SW Germany. Remarks: ¹The “Comptum” Subzone had to be re-named as Bifidatum Subzone, since the formerly name-bearing holotype of *Nautilus comptus* REINECKE, 1818 is in fact a *Pleydellia* of the Torulosum Subzone (Upper Toarcian). ²The *crassicostatum* Biohorizon corresponds to the “Comptum” Subzone auct. The former “Comptumbank” is re-named as Wilflingen-Bank, after the type locality of this bed. ³The *crassicostatum* Biohorizon is not recorded in the study area. Therefore its relative position below the *evolutum* Biohorizon is not fully verified. ⁴Contrary to DIETZE et al. (2014) we moved these previously unnamed biohorizons into the Haugi Subzone, because of the predominance of *Ancolioceras* (and very rare *Ludwigia*) therein.

The *opalinum*, *dilucidum*, *opaliniforme*, and *hansrieberi* biohorizons (Opalinum Subzone) contain specimens that show a continuous increase in size of macroconchiate *Leioceras*. Moreover, the stratigraphically younger macroconchiate *Leioceras* of the Opalinum Subzone tend to develop wavy bulges across a short sector of their flanks. Apart from these characters, the macroconchs are very similar to each other. Microconchiate leioceratids show a greater variability, some morphologies ranging over several biohorizons, as usual in other Graphoceratidae. With respect to its uniform leioceratid fauna, the interval from the *opalinum* Biohorizon up to the *hansrieberi* Biohorizon is assigned to the Opalinum Subzone.

In the *bifidatum/rieberi* Biohorizon, there is an abrupt new change in morphology and new conch sculptures

appear in leioceratids. On the one hand, there are relatively involute ammonites with a fastigate venter (group of *L. bifidatum*), and on the other hand evolute shells, which can be coarsely ribbed and which develop a rounded venter to their body chamber (group of *L. crassicostatum-evolutum*). Therefore, we include the *bifidatum/rieberi*, *uncinatum* and *evolutum* biohorizons in the Bifidatum Subzone. CONTINI et al. (1997) took the *lineatum* Biohorizon as the oldest level of the Bifidatum Subzone; however, this biohorizon is not recorded in the study area. In the *lineatum* Biohorizon, leioceratids show already a ribbing in their early ontogenetic stages.

The appearance of *Ancolioceras* immediately above the beds with the *evolutum* Biohorizon marks the Upper Aalenian (Murchisonae Zone, Haugi Subzone).

5.1. Opalinum Zone

The base of the Aalenian Stage and its oldest zone, the Opalinum Zone, is defined by the first appearance of *Leioceras opalinum* in the GSSP section at Fuentelsaz (CRESTA et al. 2001). *L. opalinum* is a common species of the *opalinum* Biohorizon at the base of the zone.

5.1.1. Opalinum Subzone

opalinum Biohorizon

Definition: The *opalinum* Biohorizon is characterized by smooth-shelled macroconchiate leioceratids with a diameter of less than 90 millimetres. Most of the microconchs correspond to *L. opalinum* and differ only in a slightly wider umbilicus or a little stronger sculpture. Atavistic morphologies recalling the ancestral genus *Pleydellia* are rare varieties. *Pleurolytoceras torulosum* is another common species of the *opalinum* Biohorizon. However, the latter species is already common in the Upper Aalenian Zone (Torulosum Subzone) of the upper Toarcian. We named this Biohorizon *opalinum* Biohorizon instead of *misera* Biohorizon, to avoid confusion between the Lower Aalenian *misera* Biohorizon sensu OHMERT & ROLF (1991) and the Late Toarcian *misera* Biohorizon sensu SCHULBERT (2001). Moreover, ammonites resembling *Pleydellia misera* have not been recorded in the study area.

We disagree with OHMERT (1993), who suggested a stratigraphic condensation of the ammonites of the ‘Torulosum-Knollen’. Our arguments against a condensation are: (1) *Pleydellia* and *Leioceras* co-occur not only in the concretions but also in the body chambers of large lytoceratids. The preservation of both is the same and hence, we conclude that they were washed in contemporaneously and are coeval. (2) Both in the sections of Mistelgau in Franconia (SCHULBERT 2001) as well as at Wittnau in the Upper Rhine Graben valley *Pleydellia* and *Leioceras* co-occur in the oldest part of the Opalinum Zone (OHMERT & ROLF 1991; OHMERT 1993; OHMERT et al. 1993; OHMERT 1996a, b). The same is true for the section of Fuentelsaz, which is the GSSP for the base of the Aalenian (GOY & URETA 1987, 1991). The accumulation of ammonites is caused by current activity on the sea bed.

Differentiation: A distinction between the *opalinum* Biohorizon and the next oldest described ammonite biohorizon is mainly based on the first appearance of the index species *L. opalinum* in the Opalinum Zone. However, there are transitional forms particularly linking *Pleydellia buckmani* and *L. opalinum* (see Chapters 4.2.2. und 4.2.3.a.). The interpretation and identification of such morphologically very similar forms is to some degree subjective and results in uncertainties in the biostratigraphical subdivision of sections.

At Wittnau (Upper Rhine Graben area), OHMERT (1993), OHMERT et al. (1993), OHMERT & ROLF (1994), and OHMERT (1996a, b) took the *pseudoarcuata* Biohorizon as the youngest biohorizon of the Torulosum Subzone (Aalenian Zone, Upper Toarcian). It yields *Cotteswoldia fluitans* (DUMORTIER), *C. burtonensis* (BUCKMAN), *Pleydellia costulata* (ZIETEN), *P. pseudoarcuata* MAUBEUGE, *P. falcifera* MAUBEUGE, and *P. misera* BUCKMAN. The absence of leioceratids clearly distinguishes this association from that of the following *opalinum* Biohorizon (= *misera* Biohorizon sensu OHMERT & ROLF) above. A study by V.D. of the rich sample from Wittnau in the LGRB showed that the

ammonite fauna of the *pseudoarcuata* Biohorizon is dominated by strong and more or less densely ribbed *Pleydellia* spp. close to *P. pseudoarcuata* (see illustrations in MAUBEUGE 1950). It is the acme of the genus *Pleydellia*. *P. cf. costulata* and *P. pseudo-lotharingica* are extreme morphologies (OHMERT & ROLF 1994). In the overlying *opalinum* Biohorizon most specimens resemble the markedly less sculptured *L. opalinum* [m] and *L. opalinum* var. *subglabrum* [M].

Based on material from the clay pit of Mistelgau near Bayreuth, SCHULBERT (2001) described the *misera* Biohorizon (non *misera* Biohorizon sensu OHMERT!) as the youngest biohorizon of the Torulosum Subzone. He considered *P. misera* and *P. buckmani* and additional rare species of *Pleydellia* as characteristic for this biohorizon. However, the association from Mistelgau differs from that of the *opalinum* Biohorizon in our study area by a markedly higher proportion of stronger ribbed and more evolute ammonites. In the *misera* Biohorizon of Mistelgau transitional forms linking *P. buckmani* and *L. opalinum* occur (SCHULBERT 2001).

At many localities of the Swabian Alb (Mögglingen near Aalen, Krumm creek at Ottenbach, vicinity of Göppingen, Metzingen, Mössingen, Bodelshausen, etc.), diverse *Pleydellia* spp. of the Torulosum Subzone are present below the occurrence of *L. opalinum*. Mostly, their phragmocones are three-dimensionally preserved in pyrite and their body chambers are compressed. However, ammonites of this interval do not occur in the study area.

dilucidum Biohorizon

Definition: The *dilucidum* Biohorizon is characterized by the chronospecies *Leioceras opalinum* β together with a mass occurrence of *Pleurolytoceras dilucidum*. In the study area it follows immediately above the range area of the ‘Torulosum-Knollenlage’. At Heiningen, its thickness expands at least 7 m above the ‘Torulosum-Knollenlage’ (AL-SAYARI 1970). We assume that the ammonoids determined by him as ‘*Lytoceras lineatum*’ from this interval mostly represent *Pleurolytoceras dilucidum*. In the Teufelsklängenbach and Pliensbach creeks the respective thicknesses of the *dilucidum* Biohorizon are unknown.

Differentiation: The next oldest *opalinum* Biohorizon differs from the *dilucidum* Biohorizon mainly by the great abundance of *Pleurolytoceras torulosum*, which has not been recorded from the *dilucidum* Biohorizon. Conversely, *P. dilucidum* is very common in the *dilucidum* Biohorizon, but extremely rare in the *opalinum* Biohorizon. The *Leioceras* fauna of the *opalinum* Biohorizon yields more *Pleydellia*-like morphologies, whereas in the *dilucidum* Biohorizon involute *L. opalinum* predominate.

opaliniforme Biohorizon

Definition: We assign the beds K 10–K 13 of KOBLER (1967, 1972) yielding the chronospecies *L. opaliniforme* to the *opaliniforme* Biohorizon. It is rarely accompanied by *Bredyia subinsignis* and *Pleurolytoceras dilucidum*. This biohorizon has been introduced by OHMERT (1993) for these beds, some tens of metres below the top of the Wasserfallschichten.

Ammonites from the Lucinenbank bed and from the levels of the Pentacrinitenplatten are so poorly preserved or rare that they can only tentatively be assigned to the *opaliniforme* Biohorizon.

Differentiation: The next older clearly distinguishable biohorizon is the *dilucidum* Biohorizon, which differs from

the *opaliniforme* Biohorizon by a much smaller adult size of the macroconchiate leioceratids and a taller whorl section. In the *dilucidum* Biohorizon, the microconchiate leioceratids are weaker sculptured than those of the *opaliniforme* Biohorizon and *L. opalinum* is much more common. There is no mass occurrence of *L. dilucidum* in the *opaliniforme* Biohorizon.

Remarks: The ‘Opalinusknohlen’ are accumulations of ammonites and bivalves formed in scour holes by bottom currents. Hydraulic sorting separated microconchs and stronger ribbed ammonites, whereas larger ammonites were obviously not affected by the currents and are thus found in the surrounding claystones. If the compaction of the mud by the weight of the overlying deposits started prior to the cementation of the pot-hole fillings, the ammonites became strongly compacted and deformed. If the lithification started before considerable compaction, the ammonites remained uncompressed.

***hansrieberi* Biohorizon**

Definition: The *hansrieberi* Biohorizon is characterized by the chronospecies *Leioceras hansrieberi*, the largest species of the genus recorded so far. Very rarely the Tethyan ammonite *Tmetoceras scissum* occurs. The *hansrieberi* Biohorizon corresponds with the *partitum* Biohorizon sensu OHMERT (1993). In the study section, it ranges from the base of the ‘Wasserfallschichten’ up to 2 m above the top of the Wasserfallbank.

Differentiation: The next older *opaliniforme* Biohorizon differs from the *hansrieberi* Biohorizon by a smaller maximum size of macroconchiate leioceratids. Only in the uppermost 4.7 m of the Wasserfallschichten leioceratids become smaller again, probably caused by unfavourable ecological conditions caused by the increased deposition of sand. Microconchiate leioceratids of the *hansrieberi* Biohorizon are in average stronger sculptured than in the *opaliniforme* Biohorizon. In the study area, *T. scissum* is only recorded from the *hansrieberi* Biohorizon.

Remarks: For the origin of the ‘Opalinusknohlen’ at the base of this biohorizon we refer to our remarks concerning the concretions of the *opaliniforme* Biohorizon.

In E France (CONTINI 1969, CONTINI et al. 1997) the first ‘horizon’ within the Bifidatum Subzone is the Horizon à Lineatum. It is characterized by the beginning of the diversification of the leioceratids: beneath *L. opalinum* and *L. lineatum*, the latter intergrading with some varieties of *L. hansrieberi*, *L. ‘comptum’* and *L. uncinatum* co-occur. In the French Jura mountains *L. lineatum* occurs somewhat earlier than *L. ‘comptum’* (CONTINI 1969). In S England (Burton Bradstock, Horn Park) the *lineatum* horizon is also characterized by *L. lineatum*, *L. ‘comptum’* and *L. uncinatum* (CALLOMON & CHANDLER 1990, 1994, CHANDLER 1995). Neither the small-sized morphology of *L. ‘comptum’* nor the coarsely ribbed morphology of *L. uncinatum* occurs in the *hansrieberi* biohorizon of SW Germany. This is the decisive reason, why we put the *hansrieberi* biohorizon still in the Opalinum Subzone. Additionally, the leioceratid faunas of the *opaliniforme* and the *hansrieberi* biohorizons are rather similar (see just above), whereas the *bifidatum/rieberi* horizon shows a clear diversification of the leioceratids. However, R. B. CHANDLER (pers. communication with V. D. in November 2020) reported, that in the *lineatum* horizon of Burton Bradstock and Symonds-bury, even if rare, the morphology of *L. hansrieberi* occurs. So we can not definitely exclude, that the smaller sized morphologies of the *L. ‘comptum’* (= *L. bifidatum*) group and the coarsely ribbed morphology of the *L. uncinatum* group occur temporarily

slightly later in SW Germany compared to E France or S England. As a consequence of this hypothetical possibility the *hansrieberi* horizon would have to be correlated with the *lineatum* horizon and would have to be regarded as the first biohorizon in the Bifidatum Subzone.

Bifidatum Subzone (= former Comptum Subzone)

***bifidatum/rieberi* Biohorizon**

Definition: The here newly introduced *bifidatum/rieberi* Biohorizon is characterized by the chronospecies *L. bifidatum*. This biohorizon comprises at least the upper part of the Bifidatumbank (bed BB-2, formerly Costosumbank). To avoid any confusion with the *bifidatum* Biohorizon of France and Southern England, which is not exactly of the same age, we named it *bifidatum/rieberi* Biohorizon.

Bed BB-1 is only tentatively assigned to this *bifidatum/rieberi* Biohorizon because ammonites are very rare in that bed and despite of intensive search we recovered only five specimens. Among them, there are two remarkably large macroconchs and the specimen figured on Pl. 18, Fig. 2a is very evolute. The few microconchs (Pl. 18, Figs. 3–5) are very close to each other in their ribbing style and not as variable as the microconchs of bed BB-2.

Since *L. ‘costosum’* cannot be used as an index fossil, we took *L. bifidatum* and *L. rieberi* as name-bearing species of this biohorizon. The use of the term *costosum-lineatum* Biohorizon (OHMERT 1993: caption of pl. 15, figs. 7, 8) appears inappropriate, since both the (invalid) *L. costosum* and *L. lineatum* are typical of older beds.

Differentiation: The *bifidatum/rieberi* Biohorizon differs from the next older *hansrieberi* Biohorizon by a replacement of the relatively uniform species *L. hansrieberi* by smaller-sized, evolute and partly stronger ribbed leioceratids. In the corresponding microconchs the variation increases as well, and their whorl sections change from oxyconic to broad, with a more rounded venter.

***uncinatum* Biohorizon**

Definition: The *uncinatum* Biohorizon is characterized by its index fossil, the chronospecies *L. uncinatum*. In the studied section, it is located in the upper part of the ‘Zopfplatten’, in the beds ZoP 5 and ZoP 6.

Differentiation: The *bifidatum/rieberi* Biohorizon differs from the *uncinatum* Biohorizon by its smaller-sized leioceratids. The leioceratid population is weaker ribbed than that of the *uncinatum* Biohorizon; especially the proportion of weaker ribbed microconchs is larger than in the *uncinatum* Biohorizon. In the *uncinatum* Biohorizon coarsely ribbed microconchs are at least similarly common than weakly sculptured ones.

***evolutum* Biohorizon**

Definition: The *evolutum* Biohorizon is characterized by its index, the chronospecies *L. evolutum*. At Bad Boll, its stratigraphic position lies within the Wilflingen-Bank and may range possibly a little down in the section.

Differentiation: The next older *uncinatum* Biohorizon is distinguishable from the *evolutum* Biohorizon by its markedly larger-sized and more involute leioceratids showing a higher whorl section, but mostly still having a fastigate venter on the body chamber, and not a rounded one typical of *L. evolutum*.

The *crassicostatum* Biohorizon is sandwiched between the *uncinatum* and the *evolutum* biohorizons (Fig. 15). Its ammonite fauna has been described by RIEBER (1963) from the western Swabian Alb. The ammonites of the *crassicostatum* Biohorizon differ from those of the *evolutum* Biohorizon by a larger size of adult specimens, the predominance of ammonites with more involute conches, and their fastigate venter.

The ammonites of the *uncinatum* Biohorizon reach larger sizes than those from the *crassicostatum* Biohorizon. In the *uncinatum* Biohorizon stronger ribbed specimens predominate both in macroconchs and microconchs and they are more involute than those from the *crassicostatum* Biohorizon.

In the beds above the *evolutum* Biohorizon abruptly appears *Ancolioceras* sp., which differs from the chronospecies *L. evolutum* by its Gothic arch whorl section, a narrower umbilicus and a weaker sculpture. The beds containing *Ancolioceras* sp. are assigned to the Haugi Subzone of the Murchisonae Zone.

Remarks: The limestone concretions of the Wilflingen-Bank containing numerous ammonites and bivalves preserved with their shells have formed rapidly and very early in diagenesis. The high carbonate content hindered the dissolution of the ammonite shells. The concretions were usually not washed out of the sediment, because they neither show borings nor incrustations typical of secondary hardgrounds. Occasional sphalerite crystals within the concretions have formed during hydrothermal activity (EFIMENKO et al. 2014).

5.2. Murchisonae Zone (Haugi Subzone)

Following DIETL (2013) but contrary to DIETZE et al. (2014) we assign beds in which *Leioceras* is at least partly replaced by *Ancolioceras*, to the Haugi Subzone (Murchisonae Zone) of the Upper Aalenian. Thus, bed AF-3 (see Figs. 10, 11) and the beds above represent the Haugi Subzone.

6. Correlations

6.1. Correlation within Germany

A. *opalinum* Biohorizon

The *opalinum* Biohorizon is recorded in the basal part of the Opalinuston Formation all over the foothills of the Swabian Alb. Since the relative proportions of *Pleydellia*-like ammonites and leioceratids of the morphospecies *L. opalinum* – “*Pleydellia*” *buckmani* is variable in different localities, the beds assigned to the *opalinum* Biohorizon might have been deposited at different times, however, not further biostratigraphically distinguishable.

The *misera* Biohorizon (sensu OHMERT & ROLF 1991; OHMERT 1993; OHMERT et al. 1993; OHMERT 1996a, b) of Wittnau (Upper Rhinegraben valley) and the *opalinum* Biohorizon of Mistelgau (SCHULBERT 2001) correlate with the *opalinum* Biohorizon of the study area.

The lower part of the Opalinum Zone of Gretenberg (near Sehnde at Hannover) (HOFFMANN 1913) corresponds approximately to the *opalinum* Biohorizon.

B. *dilucidum* Biohorizon

In the Swabian Alb, the *dilucidum* Biohorizon is additionally recorded from the clay pit at Weilen unter den Rinnen near Schömberg (ex coll. N. WANNENMACHER †, now coll. V.D.; LGRB, coll. OHMERT) and at Mössingen near Tübingen (SEILACHER et al. 1976: 330, 333).

SCHULBERT (2001) described the *dilucidum* Biohorizon from the clay pit at Mistelgau near Bayreuth (Upper Franconia). However, it remains an open question, whether it is fully identical with the *dilucidum* Biohorizon in the study area because SCHULBERT (2001) mentioned a common occurrence of *P. dilucidum* already in the *opalinum* Biohorizon, whereas this taxon is extremely rare in the *opalinum* Biohorizon in vicinity of Bad Boll. At Mistelgau, the *dilucidum* Biohorizon is restricted to the level “0 m” yielding abundant, partly extremely large-sized *P. dilucidum*. We assume that the *dilucidum* Biohorizon is widespread in the area of the Swabian and Franconian Alb despite there are no further records in the literature.

C. *opaliniforme* Biohorizon

The *opaliniforme* Biohorizon is recorded in the area between Donzdorf (DIETZE & SCHWEIGERT 2016) to Weilheim an der Teck. Most likely, it is also present in the western Swabian Alb, a few tens of metres below the ‘Wasserfallschichten’.

D. *hansrieberi* Biohorizon

This biohorizon is well recorded in the study area. Furthermore, it occurs in the Breitenbach creek at Reutlingen and in the western Swabian Alb, for instance at the Zillhausen waterfall. In northern Franconia, the *hansrieberi* Biohorizon is also present (DORN 1935).

E. *bifidatum/rieberi* Biohorizon

Up to now, the *bifidatum/rieberi* Biohorizon is only recorded in the area Gammelshausen – Boll – Weilheim an der Teck (WEBER 1964; OHMERT 1993 [OHMERT named this horizon simultaneously *lineatum* horizon and *lineatum-costosum* horizon]). In the private collection of the late N. WANNENMACHER (†, now coll. V.D.), there are a few ammonites possibly representing the *bifidatum/rieberi* Biohorizon coming from a level a few metres above the ‘Zopfplatten’ in the Steinlach creek near Mössingen. Further studies are necessary for a confirmation.

The ammonites illustrated by HOFFMANN (1913, pl. 2) from the “Costosum Subzone” of Sehnde near Hannover (northern Germany) are a convolute of more or less stronger ribbed ammonites probably coming from various stratigraphic levels. Most of them are museum’s collection material that has been subsequently assigned to the “Costosum Subzone”. Besides “*Ludwigia costosa*”, HOFFMANN (1913) mentioned numerous body chambers of

Subst.	Zone	Subzone	Biohorizons SW Germany	Biohorizonos France	Biohorizons England
Upper Aalenian (pars)	Murchisonae	Haugi	<i>opalinoides</i> yet to be worked out	<i>haugi</i>	<i>opalinoides</i>
Lower Aalenian	Opalinum	Bifidatum [ex Comptum/ Scissum ¹]	<i>evolutum</i> <i>crassicosatum</i> <i>uncinatum</i> <i>bifidatum/rieberi</i>	<i>crassicosatum/evolutum</i> ^{2,3} <i>bifidatum</i> ⁴ <i>lineatum</i>	<i>comptocostosum</i> <i>bifidatum</i> ⁴ <i>lineatum</i>
		Opalinum	<i>hansrieberi</i> ⁶ <i>opaliniforme</i> <i>dilucidum</i> <i>opalinum</i>	<i>opaliniforme</i> <i>subglabrum</i> ⁵	<i>opaliniforme</i> <i>opalinum</i>

Fig. 16. Correlation of the biohorizons in SW Germany, S England and France. Remarks: ¹In France, this subzone is called Bifidatum Subzone, in S England Scissum Subzone. Both correspond to the Comptum Subzone in the former German usage, now re-named as Bifidatum Subzone. ²A re-naming of the ‘horizon à Crassicosatum’ into the ‘horizon à Crassicosatum/Evolutum’ was necessary to avoid any confusion with the *crassicosatum* Biohorizon of the western Swabian Alb. The latter is the type horizon of *Leioceras crassicosatum*. ³The *crassicosatum/evolutum* Biohorizon does not exactly correlate with the *evolutum* Biohorizon (see Chapter 6.2). ⁴The *bifidatum* Biohorizon in France and S England is not exactly correlatable with the *uncinatum* or *bifidatum/rieberi* biohorizons (see Chapter 6.2). ⁵The French *subglabrum* Biohorizon and the *opalinum* Biohorizon are not exactly correlatable (see Chapter 6.2). ⁶For the moment we keep the Swabian *hansrieberi* and the French and Southern English *lineatum* biohorizons separated and put the *hansrieberi* biohorizon in the top of the Opalinum Subzone (see Chapter 6.2).

large-sized “*Ludwigia opalina*” from the “Costosum Subzone”. Consequently, a correlation of the *bifidatum/rieberi* Biohorizon and that “Costosum Subzone” is not possible. The large-sized body chambers of leioceratids more likely point to a correlation of the “Costosum Subzone” with the *opaliniforme* or *hansrieberi* Biohorizons.

F. *uncinatum* Biohorizon

In the entire Swabian Alb, this biohorizon is only known from the creek Teufelsklängenbach. The “Grenzbank” bed and the “Hauptmuschelbank” of northern Franconia (SCHMIDTILL 1925–1926) yields leioceratids of the Bifidatum Subzone, possibly of the *uncinatum* Biohorizon.

However, those Franconian sections and their ammonite faunas have to be re-evaluated.

G. *crassicosatum* Biohorizon

The *crassicosatum* Biohorizon is missing in the entire study area. However, it is widespread in the western Swabian Alb and adjacent Wutach area (RIEBER 1963, 1966) and also occurs in the northern Franconian Alb (SCHMIDTILL 1925–1926; DORN 1935). For the moment, we switch the *crassicosatum* biohorizon between the *uncinatum* and *evolutum* biohorizons for several reasons: The average size of the ammonites of the *crassicosatum* horizon is between the average size of the ammonites of the

uncinatum and *evolutum* biohorizons. The tendency of possessing a rounded venter on the body chamber also in smaller-sized macroconchs increases from the *uncinatum* via the *crassicostatum* to the *evolutum* biohorizon.

H. *evolutum* Biohorizon

This biohorizon is recorded with certainty only from the study area. Remarkably small-sized and evolute ammonites, which could represent this or a little older biohorizon, have been sampled from the Steinlach creek near Mössingen (coll. N. WANNENMACHER †, now coll. V.D.), from the Hohenzollern area (coll. N. WANNENMACHER †, now coll. V.D.), the Raißenbühl near Balingen-Frommern (GPIT and SMNS) and the Plettenberg near Schömburg (GPIT, SMNS) as well as from a concretion layer in the top of the Wilflingen-Bank near Gosheim (RIEBER 1963, fig. 1; SMNS). Further studies of these localities are necessary.

6.2. Correlations with other countries

A. France

Mostly based on previous studies by CONTINI (1969), CONTINI et al. (1997) subdivided the Opalinum Zone of France into five ammonite biohorizons (Fig. 16):

- The **Horizon à Subglabrum** (Opalinum Subzone) with *L. opalinum*, *L. subglabrum* and various species of *Pleydellia* correlates with the *opalinum* Biohorizon, possibly including the *dilucidum* Biohorizon.

- The **Horizon à Opaliniforme** (Opalinum Subzone) is characterized by large-sized leioceratids of the form group around *L. opaliniforme*. It corresponds to the *opaliniforme* Biohorizon, possibly including the *hansrieberi* Biohorizon.

- The **Horizon à Lineatum** (Bifidatum Subzone) is marked by the onset of a diversification in the genus *Leioceras* and thus, is regarded to be younger than the *hansrieberi* Biohorizon. In the latter, the leioceratid fauna is still morphologically rather uniform.

- The **Horizon à Bifidatum** (Bifidatum Subzone) exhibits the largest diversification within leioceratids. This favours a correlation with the *uncinatum* Biohorizon instead with the *bifidatum/rieberi* Biohorizon of the study area or an intermediate position linking both biohorizons.

- The **Horizon à Crassicostatum/Evolutum [= former Horizon à Crassicostatum]** (Bifidatum Subzone) is characterized by the disappearance of *L. bifidatum* and *L. striatum* and their replacement by strong-ribbed forms. Since the morphospecies *L. bifidatum* and *L. striatum* are still present in the *crassicostatum* Biohorizon of the Western Swabian Alb and *L. bifidatum* does not occur in the *evolutum* Biohorizon, the Horizon à Crassicostatum/Evolutum corresponds best with the *evolutum* Biohorizon,

although in SW Germany stronger-ribbed morphologies occur slightly earlier. To avoid any confusion with the slightly older *crassicostatum* Biohorizon of the western Swabian Alb, the latter being the type horizon of *L. crassicostatum*, here we re-name the French horizon à Crassicostatum into 'horizon à Crassicostatum/Evolutum'.

B. Southern England

A correlation with Southern England (CALLOMON & CHANDLER 1994; CALLOMON & CHANDLER 2009) is difficult for some intervals.

The British *Leioceras opalinum* horizon (Opalinum Subzone) corresponds to the *opalinum* Biohorizon. In Burton Bradstock (Southern England, however, the number of *Pleydellia*-like morphologies is lower than in the study area.

The British *L. opaliniforme* horizon (Opalinum Subzone) corresponds to the *opaliniforme* Biohorizon of the study area.

In contrast, the correlation of the British *L. lineatum* horizon and the *L. bifidatum* horizon with the herein newly introduced biohorizons is difficult. It is likely that the Scissum Bed of Burton Bradstock comprises time equivalents of the *bifidatum/rieberi* and *uncinatum* biohorizons. Based on observations by one of us (V.D.) we assume that the Scissum Bed of Burton Bradstock contains ammonite faunas of different ages over short distances making it almost impossible to distinguish between the beds of the *lineatum* and the *bifidatum* horizons in the field.

The British *L. comptocostosum* horizon must be younger than the *evolutum* Biohorizon, because of the high abundance of *Ancolloceras* morphologies within the chronospecies *L. comptocostosum*. Moreover, in the *L. comptocostosum* horizon the first ammonites with a *Ludwigia*-morphology appear, which are still missing in the *evolutum* Biohorizon. Because of their classification of the ammonites belonging to the genus *Leioceras*, CHANDLER & CALLOMON (2009) included the *L. comptocostosum* horizon in the British Scissum Subzone that corresponds to the Bifidatum Subzone.

C. Switzerland

MAUBEUGE (1955: pl. 2, figs. 3, 6; pl. 3, fig. 3; pl. 5, fig. 2) illustrated ammonites of the *evolutum* Biohorizon from Northern Switzerland.

ETTER (1990) studied the lower Opalinuston Formation in various outcrops of Northern Switzerland. The illustrated, strongly compressed ammonites (ETTER 1990: pl. 7, figs. 6–8; pl. 8, figs. 1–5; pl. 9, figs. 1–6; pl. 7, fig. 2) come from the *opalinum* and/or *dilucidum* biohorizons of the Opalinum Subzone.

Based on ammonite collections of BODMER and LIEB in the Natural History Museum Basel, CHRIST (1999) subdivided the Lower Aalenian of the central Swiss Jura

Mountains into four biohorizons, of which his *opalinum-subglabrum* Horizont corresponds to our *opalinum* and *dilucidum* biohorizons. A further correlation of CHRIST'S (1999) biohorizons with those in our study area is impossible having only the listed leioceratid taxa and the few illustrated specimens available.

A rich *Leioceras* fauna of the *lineatum* Biohorizon is known from Schinberg (canton Aargau) (coll. JUTZI, Schwerzenbach/CH, coll. V.D.). Further samples from various amateur collectors led us to the conclusion that the Opalinum Zone of Northern Switzerland must contain a similar number of biohorizons as in SW Germany.

D. Spain

The GSSP of the Toarcian/Aalenian boundary is located at Fuentelsaz in the Keltiberian Ranges of Eastern Spain. It is defined by the first appearance of *L. opalinum* and the onset of the Opalinum Zone in the base of bed FZ 107 of that section (CRESTA et al. 2001). The Lower Aalenian section of Fuentelsaz has been divided into the Opalinum and "Comptum" subzones. Ammonites from the c. 1.5 m-thick Opalinum Subzone and the over 20 m-thick "Comptum" Subzone of Fuentelsaz were illustrated by GOY & URETA (1987) and GOY et al. (1991, 1994, 1996). At the base of the Opalinum Subzone, *L. opalinum* and *L. lineatum* occur – both ranging up into the basal Comptum Subzone – accompanied by *P. buckmani* and *P. leura*. *L. costosum* ranges a little higher in the Opalinum Subzone. Hence, bed FZ 107 correlates with the *opalinum* Biohorizon. A further subdivision of the Opalinum Subzone is impossible. The basal part of the "Comptum" Subzone with the last occurrences of *L. lineatum* and *L. opalinum* most likely corresponds to the *lineatum* Biohorizon of Southern England and France. A correlation of the higher up-section with the *bifidatum/rieberi*, *uncinatum* or *crassicosatum* biohorizons is not possible and any ammonites indicative of the *evolutum* Biohorizon are unknown from Fuentelsaz.

URETA GIL (1983: pl. 3, figs. 2–11; pl. 4, figs. 1–12) described an ammonite fauna of the "Sz Comptum" from the Keltiberian Ranges of Eastern Spain, which corresponds very well with the *bifidatum/rieberi* Biohorizon of Southwestern Germany.

E. Further important records in Europe

In the section of Bakonycsérnye (Hungary), GÉCZY (1967) distinguished a "Zone à *Leioceras opalinum*" and a "Zone à *Leioceras comptum*". He illustrated numerous leioceratids, especially of the "Zone à *L. comptum*". In Italy, sections of the Opalinum Zone are mostly incomplete or strongly condensed. Leioceratids of the Opalinum Zone have been reported, for instance from the Southern Alps (VACEK 1886) and from Sicily (GEMMELLARO 1886; PALLINI et al. 2004).

SAPUNOV (1970) described leioceratids from a condensed level comprising the Opalinum and "Comptum" subzones in Bulgaria.

7. Additional macrofauna of the Opalinuston Formation

The macro- and microfauna of the Opalinuston Formation at the Toarcian/Aalenian transition of Switzerland was exhaustively described by ETTER (1990). The macrofauna of the Opalinuston Formation in Franconia was studied by KUHN (1935). More recently, HEGELE (1995) provided an updated list of the Opalinuston fauna and flora. For the macrofauna of the *hansrieberi* Biohorizon, we mainly refer to DIETZE & SCHWEIGERT (2018).

Nautiloids. – Nautiloids are rare in the Opalinuston Formation of the study area. They occur both in the basal beds of the formation (*opalinum* Biohorizon; Pl. 27, Fig. 1) as well as in the beds of the *hansrieberi* and *bifidatum/rieberi* biohorizons. Recently identified as *Ligeiceras jureense* (QUENSTEDT) (DIETZE & SCHWEIGERT 2018), this smooth-shelled nautiloid species should be labelled as *Metacenoceras jureense* (QUENSTEDT) because the genus *Ligeiceras* BARROSO-BARCENILLA et al., 2011 is a subjective junior synonym of *Metacenoceras* TINTANT, 1984. Both genera have different type species, but the same set of species.

Belemnites. – Belemnite rostra have been recorded especially from the *opalinum* and *hansrieberi* biohorizons and from the belemnite breccia in the upper part of the Zillhausen Member. In the *opalinum* and *dilucidum* biohorizons, morphologically highly variable clavate forms such as *Hastites clavatus* (SCHLOTHEIM) (Pl. 27, Fig. 2) and *Hastites subclavatus* (VOLTZ) dominate, rarely accompanied by species of *Acrocoelites* (Pl. 27, Fig. 3) and *Mesoteuthis*. In the Zillhausen Member, *Hastites* spp. has become extinct.

Bivalves. – In the basal part of the Opalinuston Formation (*opalinum* and *dilucidum* biohorizons) shallow-infaunal taxa such as *Palaeonucula hammeri* (DESHAYES) (Pl. 27, Fig. 7), *Ryderia doris* (ORBIGNY) (Pl. 27, Fig. 6), *Nicaniella voltzi* (GOLDFUSS) (Pl. 27, Fig. 8), and *Cucullaea* sp. occur. Some beds contain the pseudoplanktonic *Pseudomytiloides dubius* (SOWERBY) (Pl. 27, Fig. 9) and *Lios-trea erina* (ORBIGNY) as well as the probably epibenthic or nektoplanktonic *Bositra buchi* (RÖMER) (Pl. 27, Fig. 4), thus somewhat resembling the bivalve fauna of the Posidonia Shale. *Pseudomytiloides* and *Lios-trea* were probably attached to larger ammonite shells or driftwood. For a discussion of the supposed lifestyles of these taxa, see ETTER (1996). The lucinid *Mesomiltha plana* (ZIETEN) (Pl. 28, Fig. 4) with its supposed chemosymbiotic living

style (see below) is very common in the Lucinenbank and seems to be restricted to this single bed, thus pointing to very special environmental conditions during the formation of the Lucinenbank. In the same bed, the trigoniid *Scaphotrigonia navis* (LAMARCK) (Pl. 28, Fig. 1) appears for the first time, accompanied by a few other infaunal taxa (*Pleuromya*, *Unicardium*). In contrast to eastern France and Franconia, earlier trigoniids are unknown from Swabia (LEBKÜCHNER 1932, and own observations). Higher up, in the level of the ‘Pentacrinitenplatten’, isolated valves of juvenile *Scaphotrigonia navis* (LAMARCK) are common (Pl. 20, Fig. 4), together with valves of byssate species such as *Oxytoma inaequalis* (SOWERBY), *Chlamys textoria* (SCHLOTHEIM), and other pectinids. In the concretions of the *opaliniforme* Biohorizon, specimens of medium-sized infaunal bivalves occur (*Goniomya*, *Protocardia*, *Quenstedtia*; Pl. 28, Fig. 6). In the beds of the *hansrieberi* Biohorizon, the deep-infaunal *Scaphotrigonia navis* (LAMARCK) (Pl. 28, Figs. 2, 5) becomes rather abundant, often represented by adult double-valved specimens still in life position, and other infaunal taxa such as *Pronoella trigonellaris* (SCHLOTHEIM) (Pl. 28, Fig. 3), aside species of *Goniomya*, *Pleuromya*, and *Gresslya*.

Gastropods. – The aporrhaid *Toarctocera subpunctata* (MÜNSTER) is very common and widespread in the basal part (*opalinum* and *dilucidum* biohorizons) of the Opalinuston Formation (BRÖSAMLEN 1909; GRÜNDEL et al. 2009; SCHULBERT & NÜTZEL 2013; SCHWEIGERT 2015; Pl. 27, Fig. 5). Higher up in the section, this taxon has not been recorded along with the co-occurring *Cryptaulax armata* (GOLDFUSS), *Amphitrochus duplicatus* (SOWERBY), *Costat-rochus subduplicatus* (ORBIGNY), and *Eucycloidea tenuistria* (MÜNSTER in GOLDFUSS). Other gastropod taxa from the basal part of the Opalinuston Formation of the study area have been reported by BRÖSAMLEN (1909), including the rare *Neritopsis opalina* BRÖSAMLEN. In the Zillhausen Member, gastropods are generally rare, comprising *Turritelloidea opalina* (QUENSTEDT) (see GRÜNDEL 2005) and pleurotomariids (SIEBERER 1907).

Crustaceans. – Decapod crustaceans rarely occur in concretions of the *hansrieberi* Biohorizon, mostly represented by glypheid lobsters. ETTER (2004) reported further crustacean taxa including isopods and tanaidaceans from the Opalinuston Formation of Switzerland; however, none of these have been recorded yet in the study area.

Echinoderms. – Identifiable crinoids are restricted to the level of the ‘Pentacrinitenplatten’, where columnals of *Chariocrinus wuerttembergicus* (OPPEL) form thin lenses (SIEVERTS-DORECK 1964; WETZEL & MEYER 2006). In eastern Swabia, complete crowns of this crinoids have been reported in the the same stratigraphic position (SIEVERTS-DORECK 1983). No other macro-remains of echinoderms are known from the Opalinuston Forma-

tion of the study area. Further north-east, at Ottenbach, a well-preserved starfish (?*Terminaster*), probably part of a mass occurrence, was found in a piece of claystone of the Teufelsloch Member (SCHWEIGERT 2011).

Brachiopods. – Due to the prevailing soft-bottom conditions, brachiopods are extremely rare in the Opalinuston Formation. Besides juvenile rhynchonellids, the inarticulate *Disciniscia paparacea* (MÜNSTER in GOLDFUSS) occurs, which probably had a pseudoplanktonic living style being attached to ammonite shells (ETTER 1996).

Vertebrates. – Vertebrate remains sporadically occur in limestone concretions of the basal part of the Opalinuston Formation. Recently, articulated remains of ichthyosaurs (*Stenopterygius aalenensis* MAXWELL et al., 2012) as well as the unique skull of a metriorhynchoid crocodile (*Opisuchus meieri* AIGLSTORFER et al., 2020) and a large ray-finned fish (*Dapedium ballei* MAXWELL & LÓPEZ-ARBARELLO, 2018) have been reported. In addition, there is an unpublished specimen of a giant ichthyosaur (*Suevoleviathan* sp., SMNS, leg. G. GEBHARD) and a skull of the elongate ray-finned fish *Saurostomus* sp. (SMNS, leg. G. SCHWEIGEL); both specimens originate from the *opalinum* Biohorizon of Heiningen.

8. Some aspects of petrography, geochemistry and sedimentology of the Teufelsloch Formation in the Teufelsloch section

8.1. Petrography

In June 2020, three of us (V.D., M.F., G.S.) visited the most relevant localities for final measurements and discussions concerning the lithological interpretation. M.F. took four rock samples (Opaliniforme-Schichten, Wasserfallschichten, Opalinuston 4 (= Op 4 in Fig. 2), basal Achdorf Formation), which were analyzed in the laboratory of the LGRB. There is a striking discrepancy between the high content of clay minerals and the relatively low content of clay-sized particles; however, based on microscopic analyses of the samples, the claystones do not contain any coarse-sized particles. The likelihood is that these unexpected records of a coarse fraction of particles results from undispersed aggregates of clay minerals, hence, this effect has been corrected in our final analytical data.

A. Analysis of sample 1 taken c. 1 m below the reddish-brown, somewhat silty layer within layer K10 in the Opaliniforme-Schichten.

Silt-claystone, weakly calcareous, with fine mica;

Composition: Clay minerals 61 %, quartz 26 %, calcite 10 %, feldspar 3 %

Grain size distribution (corrected): 33.3 % clay (< 0.002 mm), 66.7 % silt (0.002–0.063 mm).

B. Analysis of sample 2, taken just below the base of the Wasserfallbank (Wasserfallschichten)

Silt-claystone, weakly calcareous, weakly fine-sandy, fine mica, flaser to cross bedding;

Composition: Clay minerals 57 %, quartz 31 %, calcite 9 %, feldspar 3 %

Grain size distribution (corrected): 20 % clay (< 0.002 mm), 65 % silt (0.002–0.063 mm), 15 % fine sand (0.063–0.2 mm).

C. Analysis of sample 3 from the top of Op-4a (Opalinuston 4)

Siltstone, clayey, fine-sandy, weakly calcareous, laminated;

Composition: Clay minerals 46 %, quartz 41 %, calcite 10 %, feldspar 3 %

Grain size distribution (corrected): 26 % clay (< 0.002 mm), 55 % silt (0.002–0.063 mm), 19 % fine sand (0.063–0.2 mm).

D. Analysis of sample 4 from directly above the Wilflingen-Bank (Achdorf Formation)

Siltstone, fine-sandy, weakly clayey, flaser bedding, bioturbated;

Composition: Clay minerals 46 %, quartz 48 %, calcite 10 %, feldspar 3 %

Grain size distribution (corrected): 22.5 % clay (< 0.002 mm), 57.5 % silt (0.002–0.063 mm), 20 % fine sand (0.063–0.2 mm).

8.2. Sedimentology and geochemistry

A. Range area of the ‘Torulosum-Knollenlage’ and ‘Dilucidum-Schichten’

The concretions (‘Torulosum-Knollen’) were formed at the storm wave base (OLIVERO 2007). The gypsum in the ammonites in the upper ‘Torulosum-Knollenlage’ has formed during recent weathering processes.

B. Lucinenbank

The levels with siderite concretions some meters below the Lucinenbank exhibit in cross-section small-scale ripples and lamination and hence, represent distal tempestites (e.g., WETZEL & ALLIA 2003).

The typical Lucinenbank represents a grain- to rudstone composed of variable amounts of crinoid debris, (fragmented) mollusc shells including disarticulated shells of the lucinid bivalve *Mesomiltha plana*, and dark grey, irregular-shaped to spherical, micritic limestone nodules a few millimetres to centimetres in size within a fine-grained marl or pyrite-bearing limestone matrix (Fig. 6 B, C). These nodules contain considerable amounts of pyrite, disseminated within the concretion interior or concentrated along the margin. The components con-

stituting the Lucinenbank exhibit a grading as crinoid debris is enriched at the base and exhumed nodules and (fragmented) shells constitute the upper part of the bed (Fig. 6B). The lithology of the Lucinenbank varies laterally from an about 5 cm-thick limestone bed rich in mollusc shells associated with cone-in-cone structures (Fig. 6B) to a 1–2 cm-thick bioclast-rich interval covering a nodular limestone (Fig. 6C). The Lucinenbank (= Layer 3) needs to be interpreted in context with the interval underneath, comprising two horizons (layers 1, 2) with ellipsoidal concretions flattened parallel to bedding (Fig. 6A). The concretions in the upper layer (= Layer 2) exceed 10 cm in lateral extent whereas the deeper ones (= Layer 1) are somewhat smaller. The Lucinenbank interval documents a considerable episode of omission and repeated sediment reworking by at least 3 successive sediment winnowing to reworking episodes.

When growing by diffusion, stratabound concretions of the encountered size need to reside within the same geochemical zone for several hundreds to more than thousands of years (e.g., RAISWELL & FISHER 2004; BLOUET 2020 pers. comm.) and hence, mark a sedimentary hiatus (WETZEL & ALLIA 2000). Given that the concretion size corresponds to the duration of the sedimentary hiatus, the Layer 1 concretions formed during a shorter time span than those in Layer 2. However, currents causing the hiatus were too weak to exhume the nodules. In contrast, during formation of Layer 3, first, currents removed crinoids living in a supposedly somewhat elevated area from their substrate (e.g., WETZEL & MEYER 2006). Later, currents reworked an at least 10 cm-thick sediment layer as indicated by the enrichment of the lucinid shells and some small-sized concretions that were bored when exposed on the seafloor. In modern, organic-rich, shallow-marine sediments, similar-sized lucinids live closely above the sulfate reduction zone in about 3–10 cm sediment depth or more (e.g., STANLEY 1970). Without exception, lucinids are chemosymbiotic, ‘sulfide-mining’ organisms (TAYLOR & GLOVER 2006). The sulphide is taken via tubes produced by the bivalve downward and processed in its gills by symbionts that provide nutrition (TAYLOR & GLOVER 2006). Consequently, sulfide must have been available within the reach of the lucinids probably in the range of a few centimeters or more (e.g., STANLEY 1970). The exhumed nodules, therefore, must have formed below the lucinids or somewhat deeper within the sulfate reduction zone, maybe 10–15 cm. Currents reworked this interval. With time, the number of exhumed nodules increased and paved the seafloor together with exhumed shells and hence, prevented further erosion. The lateral lithological variability of the Lucinenbank implies that the seafloor was structured by a relief. Consequently, the layers 1–3 document an increasing intensity of bottom current reworking. However, after formation and burial of Layer 3, deposition was

still retarded for some time during that cementation within the sulfate reduction zone took place as indicated by pyrite impregnation of the matrix. The development of cone-in-cone limestone layers remains to be resolved.

C. Levels of the ‘Pentacrinitenplatten’

The crinoid accumulations are caused by storm events and form small, laterally thinning lenses (WETZEL & MEYER 2006).

D. Opaliniforme-Schichten

The sampled concretions of layer K 9 exhibit on all sides, up to 2 cm deep and 0.8 cm wide *Gastrochaenolites* borings being truncated to a varying degree. They are filled with marl and some contain the still articulated shells of the producers. Locally, only preserved within depressions, oysters are attached to the nodules. Thus, this interval documents an episode of sediment reworking and omission. Prior to exhumation of the nodules, sediment deposition was retarded to allow their formation (e.g., WETZEL & ALLIA 2000; see above). Later, the concretions became exhumed by currents and bored by the *Gastrochaenolites* producers. The currents were strong enough to turn the nodules and to cause their partial abrasion. When the amount of suspension increased, oysters adapted to live in muddy water settled on the nodules. Before final burial, currents accelerated and partly removed the oysters.

Further up, about 30 cm below the fossil-rich bed K10, another horizon with stratabound concretions marks a sedimentary discontinuity. These nodules may reach a size of several centimeters and rarely contain fossils. The concretions appear to be genetically related to the fossil-rich layer at the base of bed K10, as winnowing currents enriched the shells and retarded deposition for a period of time sufficient for concretion formation (e.g., RAISWELL & FISHER 2004; BLOUET 2020, pers. comm.).

Within bed K10, the different layers with concretions may represent different stages of repeated sediment reworking, as elsewhere in this section. The Opalinusknollen-type concretions probably formed after storms when combined flow enriched fossils in pot-casts (e.g., CHEEL & LECKIE 1993; OLIVERO 2007). The stratabound limestone concretions containing no or only few fossils were not exhumed, but nonetheless represent simple sedimentary hiatus (see above).

E. Belemnite Breccia

The Belemnite Breccia is intercalated in typical, dark-grey, platy Opalinuston mudrock and marks another sedimentary discontinuity. The Belemnite Breccia represents a rudstone composed of (fragmented) mollusc shells, locally high concentrations of belemnite rostra, and two

types of exhumed concretions embedded in marly limestone; (1) large, ellipsoidal, light brownish-beige nodules, 5 cm high and >15 cm wide, and (2) flat, dark-grey to black, pyrite-bearing limestone concretions up to 6 cm in size that occasionally exhibit *Gastrochaenolites* borings, up to 1.5 cm deep and 0.5 cm wide.

The brownish concretions exhibit locally small-scale current ripples, but mainly bioturbational structures that show a succession indicative of progressive substrate induration; (1) indistinct bioturbational/biodeformational structures that disturb the original bedding, (2) *Phycosiphon*, (3) *Planolites*-like burrows, (4) *Chondrites*, and (5) probably *Rhizocorallium* (e.g., WETZEL 2015). The first two burrow types (Suite-1) contain material similar to the concretion body whereas the latter traces (Suite-2) are actively filled with the dark marl housing the concretions (= matrix of the Belemnite Breccia). Both Suite-1 and Suite-2 burrows are truncated at the surface of the nodules. Obviously, the locally preserved small-scale cross-bedding records the depositional currents. The Suite-1 burrows document the colonization of this muddy event bed (e.g., WETZEL & UCHMAN 2001; CELIS et al. 2018). The dark marl filling the Suite-2 traces implies burial of the horizon wherein these concretions grew but they still resided within the bioturbated zone and became increasingly cemented. Below, in the sulfate reduction zone, the dark limestone concretions probably formed at the same time.

The onset of bottom current activity and hence, the slow-down of deposition appears to be recorded by ripple formation, followed by omission documented by the bioturbation structures indicating progressive induration of the brownish nodules, while the dark concretions grew below. Then both types of concretions became exhumed, transported, and embedded within the lag deposits. Obviously, the limestone concretions were more indurated than the brownish nodules, as indicated by *Gastrochaenolites* borings compared to the not-bored brownish nodules exhibiting truncated burrows. The bottom currents were locally and temporarily so fast that only belemnite rostra accumulated.

F. Level of the ‘Zopfplatten’

The upper part of the Zopfplatten interval (ZoP 5, 6) exhibit typical hummocky cross-stratification characterized by a wave-length of 1–1.5 m and an amplitude of 10–15 cm that is typical of tempestites (e.g., CHEEL & LECKIE 1993). These beds formed slightly above storm-wave base in a water depth of c. 30 m or less (WETZEL & ALLIA 2003). They consist of fine-sand laminae separated by thin dark mud veneers and contain locally greyish ellipsoidal limestone concretions up to 3–4 cm wide and 2–3 cm high having their long axis inclined to bedding. The sand laminae are bent around and do not crosscut the

exhumed concretions and hence, indicate transport of the latter during the storm. The dark muddy interlayers were preferentially reworked by producers of *Chondrites*. These traces continue into the concretions. Therefore, the concretions were only slightly lithified when they became exhumed during a storm, otherwise the *Chondrites* burrows would not continue from the surrounding sediment into the nodules. This observation provides striking evidence that concretion formation was a slow process (see above) and nodules forming near the sediment surface were only partially, but sufficiently cemented to be resistant against compaction but still in a plastic state (WETZEL 1992).

G. Transformation of the (white) aragonitic shell into (brown) calcitic shells of the fossils

Within the Opalinuston ammonites with white, aragonitic shells occur from the base up to -4.9 m below the top of the Wasserfallschichten, whereas further up, the ammonite shells consist of brownish calcite (e.g., ANDALIB 1973). Within a thin transitional extent of strata, ammonite shells may show partial replacement of aragonite by calcite starting from the outer surface (ANDALIB 1973). Both aragonite as well as calcite crystals are 3–5 μm in size. The preservation of the original shell mineralogy, in particular of metastable aragonite, appears to depend on several factors; most important are (1) reducing conditions within the host sediment (HALL & KENNEDY 1967), (2) low permeability of the host sediment (HALL & KENNEDY 1967; ANDALIB 1973; JANISZEWSKA et al. 2018), and (3) seawater composition at the time when the aragonitic fossils became embedded.

Reducing conditions within the sediment maintain the protective effect of the organic skeletal matrix (HALL & KENNEDY 1967). Within the claystones of the Opalinuston, reducing conditions developed at shallow levels within the sediment as evidenced by the occurrence of (i) dark color (e.g., MYROW 1990), (ii) a relatively high organic carbon content $>0.2\%$ (e.g., NAGRA 2008), (iii) the recurrent presence of the trace fossil *Chondrites* (e.g., BROMLEY & EKDALE 1984), (iv) framboidal pyrite (e.g., LEROUGE et al. 2014; LAUPER et al. 2018; TAYLOR & MACQUAKER 2000), and (v) early diagenetic concretions formed within the sulfate-reduction zone (e.g., WETZEL & ALLIA 2000).

Low permeability prevents movement of fluids and retards diffusion such that both can cause mineral transformation if pore water composition changes. In fact, the Opalinuston Formation exhibits a very low permeability in the range of $10^{-13} \text{ m s}^{-1}$ in the compacted state (e.g., NAGRA 2008). This is mainly caused by the high clay content that may exceed 60% in the lower part of the formation whereas towards the top the clay content may decrease to 35–40% and less as determined about 130 km to the SSW of the studied site in the well Benken (Switzerland; NAGRA 2008). Palaeogeographically relative to

Benken, the studied site is located more proximally to the basin (e.g. ZIEGLER 1990). The above given lithologic data are confirmed by our analyses (see section 8.1).

During the Aalenian, inorganic precipitation of aragonite was facilitated by the Mg:Ca ratio of seawater >2 , whereas during the Bajocian–Bathonian it shifted to <2 fostering inorganic calcite precipitation (e.g., LOWENSTEIN et al. 2001). The original $\text{Mg}^{2+}:\text{Ca}^{2+}$ ratio of seawater was very likely kept during early diagenesis and transformation of aragonite to calcite was hindered (e.g., FERNÁNDEZ-DÍAZ et al. 1996) due to the low permeability of the host sediment.

In the studied section a few metres below the Wasserfallschichten, the sand content increases on the expense of the clay content as sediment reworking by waves and currents becomes more frequent as indicated by coarse-grained layers, chamositic oolites, and horizons containing exhumed early diagenetic concretions and, finally, by the Eisensandstein Formation (e.g., FRANZ & NITSCH 2009). The Wasserfallschichten already contain up to 25% sand in the decalcified sediment fraction (ANDALIB 1973). The increased sand content caused an increasing permeability facilitating downward diffusion of seawater having a $\text{Mg}^{2+}:\text{Ca}^{2+}$ ratio <2 since the Bajocian, favoring calcite precipitation (e.g., LOWENSTEIN et al. 2001). This interpretation is supported by experimental evaluation of diffusion in compacted Opalinuston mudrock showing differences between the basal and top interval of the Opalinuston, being somewhat higher and lower, respectively (e.g., DEGUELDRE et al. 2003). The boundary between preserved aragonitic and replaced calcitic ammonite shells evidently depends on mudrock properties and thus, may vary locally in depth below the top of the Wasserfallschichten, as already mentioned by ANDALIB (1973).

9. Results and conclusions

After CRESTA et al. (2001) and MÖNNIG et al. (2016), the Aalenian Stage has a duration of c. 3.5 million years (180 Ma–176 Ma). The Opalinum Zone, which corresponds to the deposition of the Opalinuston-Formation, has duration of 600.000 years (CRESTA et al. 2001). Taking into account the eight distinguishable biohorizons of the Opalinum Zone in SW Germany, seven of which were recognized in the Teufelsloch section (Fig. 15), this means an approximate duration of 75.000 years per biohorizon.

The evolution of leioceratids in the Opalinum Subzone (Teufelsloch Member and base of Zillhausen Member) allows discrimination into four biohorizons (*opalinum*, *dilucidum*, *opaliniforme* and *hansrieberi* biohorizons) based upon an increase in size and a tendency towards coarser ribbing. Up to the base of the Wasserfallschichten, the claystones are quite uniform. Thus, the increase in size

of leioceratids was apparently not affected by the amount of suspension in the water, but by other factors, possibly an increase of the carbonate content or some autecological processes. At the base of the Zillhausen Member, which coincides with the base of the *hansrieberi* Biohorizon, leioceratids reach the largest adult diameters of the genus as interpreted here. Coupled with an increase in sand supply, size decreases and increases again two metres above the sandy Wasserfallbank.

In the chamositic Bifidatumbank, leioceratids abruptly become smaller-sized and stronger ribbed. If size directly corresponds with living conditions including food quality, we must assume deterioration, possibly caused by a shallowing water depth to only 20–30 m instead of c. 50 m during the deposition of the Teufelsloch Member (WETZEL & ALLIA 1996, 2000, 2003; WETZEL et al. 2003). More frequently, firm beds and temporary omission surfaces formed in the section, due to increasing winnowing documented by an increase in the carbonate and/or sand content. In the upper part of the ‘Zopfplatten’ (ZoP 5) leioceratids increase a little in size and ribbing strength (*uncinatum* Biohorizon). In the next younger *crassicos-tatum* Biohorizon, which is missing in the study area, the ammonites decrease in size again (cf. RIEBER 1963, 1966). This trend continues towards the *evolutum* Biohorizon of the terminal Opalinum Zone. Leioceratids of the *evolutum* Biohorizon are weaker sculptured than those of the *uncinatum* Biohorizon and have a typically rounded venter.

About 1–2 m above the beds of the *evolutum* Biohorizon ammonites of the genus *Ancolioceras* appear abruptly and predominant ?*Leioceras* sp. *Ancolioceras* specimens exhibit a fastigate venter. We question a direct evolution from the chronospecies *Leioceras evolutum* with a rounded venter to the genus *Ancolioceras* with a fastigate venter. It is more likely that a special evolution leading to *Ancolioceras* took place in another Jurassic basin (? Southern England and adjacent areas) and subsequently, these forms migrated into the study area, leading to the suppression of native ammonites of the genus *Leioceras*. However, the latter probably evolved to the similarly wide-sectioned and markedly ribbed genus *Ludwigia* (RIEBER 1963; CHANDLER & CALLOMON 2009).

The Opalinuston Formation is a good example of excellent time resolution of a lithological succession by means of ammonite biostratigraphy. The prerequisite is an extraordinarily rapid evolution of some ammonite genera – in terms of geological time scale – in this case of the genus *Pleydellia*, with latest representatives in the basal Opalinuston Formation (only locally) and its evolution to *Leioceras*.

We concur with the observation that Tethyan immigrants are restricted to a few stratigraphic levels and that they are completely absent in other beds of the Opalinuston Formation (SCHWEIGERT 1996). Ammonites of the

genus *Bredya* occur in the *opalinum*, *dilucidum* and *opaliniforme* biohorizons, whereas *Tmetoceras* has only been recorded yet from the *hansrieberi* Biohorizon (RIEBER 1963; DIETZE & SCHWEIGERT 2018) and from the *crassicos-tatum* Biohorizon (RIEBER 1963, 1966).

Acknowledgements

This study was only possible by the generous support of numerous amateur palaeontologists and scientists. Our greatest thanks go to ERICH SCHNEIDER (Heiningen) and THOMAS BALLE (Alfdorf) for sharing their detailed knowledge of the sections exposed in the Teufelsklingsbach and Pliensbach creeks; their information helped a lot especially for our initial orientation in the field. Moreover, they donated numerous ammonites collected bed-by-bed, and, together with ANDREAS HOFBAUER (Wendlingen), they helped us in the field and with the preparation of the material. NORBERT WANNENMACHER (†) discussed continuously our preliminary results and prepared some of the ammonites. ROBERT B. CHANDLER (The Natural History Museum, London, United Kingdom) is acknowledged for discussions on the taxonomy of leioceratids. JEAN-PHILIPPE BLOUET (Brussels) provided detailed information about rates and timing of concretion growth based on geochemical modeling. Furthermore, we have got support related to this project by WOLFGANG DANGELMAIER (Lauterstein-Nenningen), MATTHIAS GRUPP (Göppingen-Holzheim) and the late HANS KLASCHKA. BERNHARD HOSTETTLER (Natural History Museum Bern, Switzerland) and INGMAR WERNEBURG (Palaeontological Collection at Eberhard Karls University, Tübingen) kindly loaned specimens from the collections under their care. GERNOT ARP (Geoscience Centre, University of Goettingen), ANTON HEGELE (Göppingen) and CHRISTIAN SCHULBERT (Geozentrum Nordbayern, Friedrich-Alexander University Erlangen-Nürnberg) helped with access to rare literature. Finally, we are grateful for the constructive reviews by ROBERT B. CHANDLER (The Natural History Museum, London, United Kingdom) and BERNHARD HOSTETTLER (Natural History Museum Bern, Switzerland), which greatly improved our manuscript.

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Manuscript received: 18 October 2020, revised version accepted: 14 December 2020.

Plate 1

(1, 3): *Pleurolytoceras torulosum* [m], (1) NMBE 5024894 [61], (3) NMB 5024901b [66]. (2, 5, 6): *L. opalinum* α var. *subglabrum* [M], (2) NMB 5024902 [64], (5) GPIT/CP/21178, (6) GPIT/CP/21179. (4): *L. opalinum* α var. *comatum* [m], (4) NMB 5024901a [66], (7, 9, 10, 13) *L. opalinum* α var. *buckmani* [m], (7) NMB 5024903 [65], (9) NMBE 5024904 [68], (10) GPIT/CP/21180, (13) GPIT/CP/21181. (8) *L. opalinum* α var. *leurum* [m], GPIT/CP/21182. (11): *L. opalinum* α [m], GPIT/CP/21183. (12): *L. opalinum* α var. *subcostosum* [m], GPIT/CP/21184. (14): *L. opalinum* α var. *tomum* [m], GPIT/CP/21185. (15): *L. opalinum* α var. *costulatum* [m], NMB 5024938 [164]. (1–15) Teufelsklingenbach at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, range area of the Torulosum concretion layer; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opalinum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

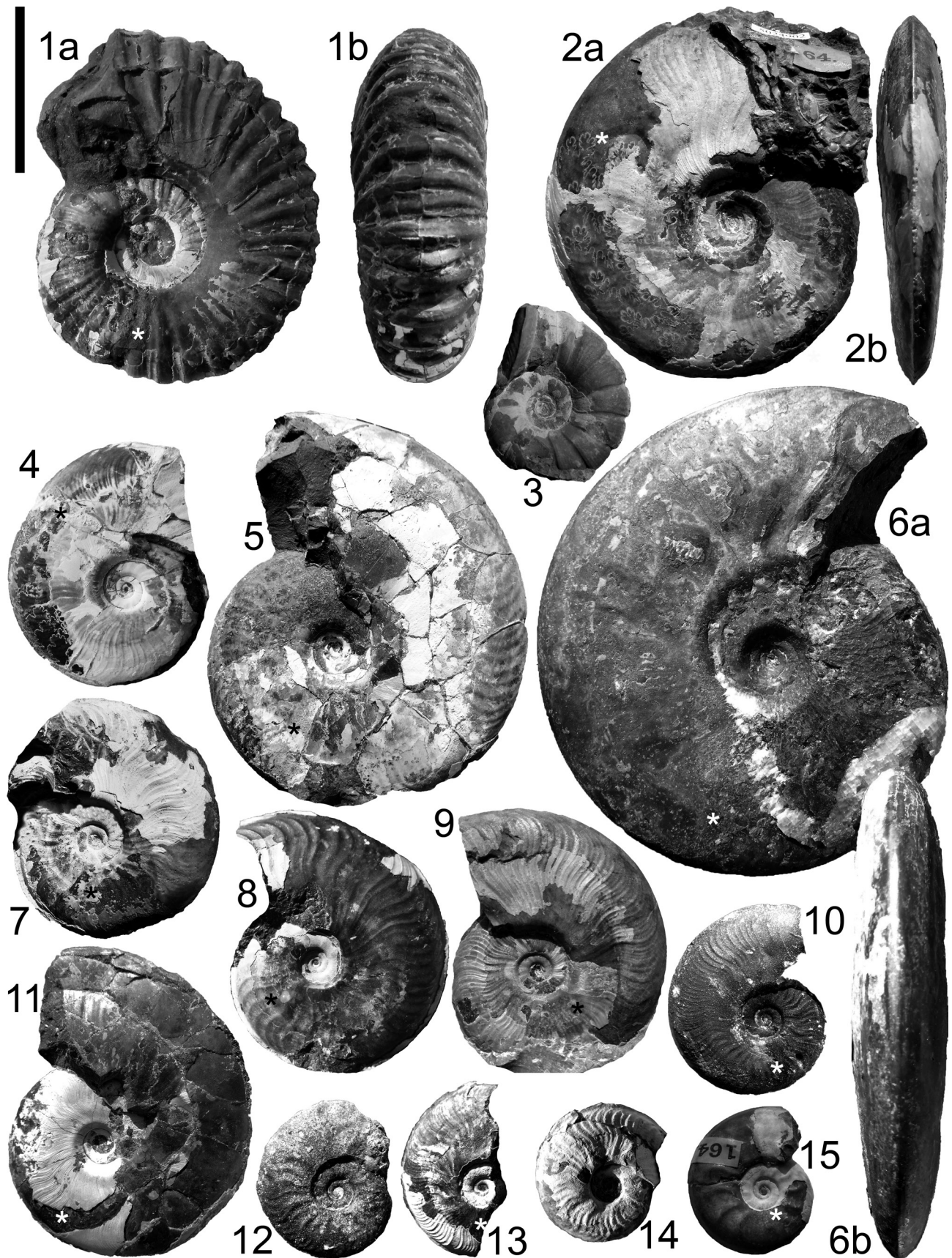


Plate 2

(1): *Pleurolytoceras torulosum* [m], SMNS 70608/51. (2, 3): *L. opalinum* α var. *comatum* [m], Pliensbach creek, (2) SMNS 70608/52, (3) SMNS 70608/53. (4, 5, 10): *L. opalinum* α var. *subglabrum* [M], (4–5) Pliensbach creek, (4) SMNS 70608/54, (5) SMNS 70608/55, (10) SMNS 70608/56, eastern tributary of the Pliensbach creek. (6): *L. opalinum* α var. *leurum* [m], GPIT/CP/21186; Teufelsklingsbach creek. (7, 8) *L. opalinum* α [m], Pliensbach creek, (7) SMNS 70608/57, (8) SMNS 70608/58, Teufelsklingsbach creek. (9): *Pleurolytoceras torulosum* [m], SMNS 70608/59, eastern tributary of the Pliensbach creek. (11): *L. opalinum* α var. *buckmani* [m], SMNS 70608/60, eastern tributary of the Pliensbach creek. (1–11) Opalinuston Formation, Teufelsloch Member, range area of the *Torulosum* concretion layer; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opalinum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

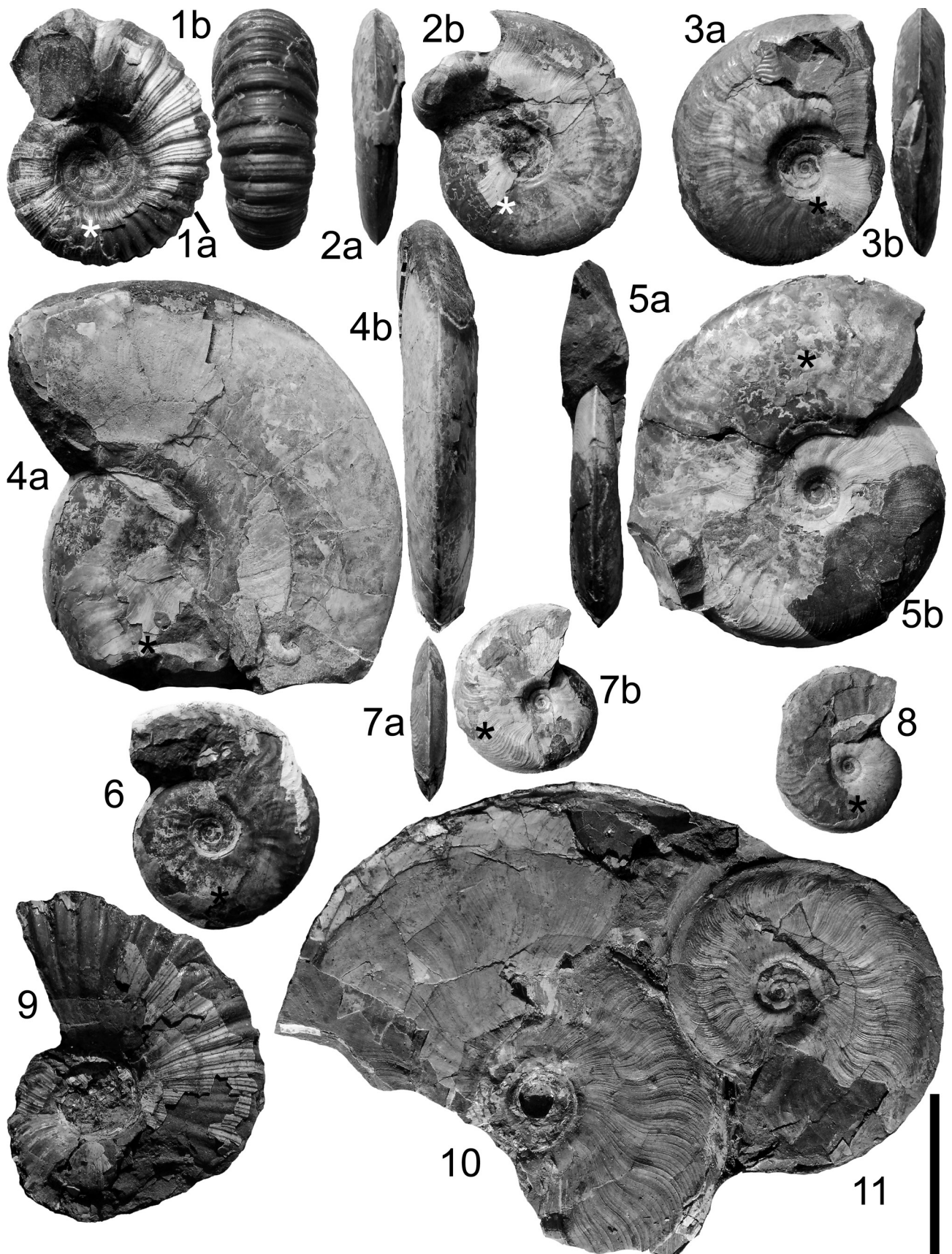


Plate 3

(1): *Leioceras opalinum* [?m], cast of holotype, from the vicinity of Steglitz at Altenbanz (Upper Franconia, Bavaria), basal Opalinuston Formation; original in the Naturkunde-Museum Coburg, Reinecke Collection no. 50; SMNS 70608/61. (2–3, 6, 10, 12): *L. opalinum* β [m], (2) SMNS 70608/62, (3) SMNS 70608/63, (6) SMNS 70608/64, (10) SMNS 70608/65, (12) SMNS 70608/66. (4, 5, 7): *L. opalinum* β var. *buckmani* [m], (4) SMNS 70608/67, (5) SMNS 70608/68, (7) SMNS 70608/69. (8, 11): *L. opalinum* β var. *undatum* [m], (8) SMNS 70608/70, (11) SMNS 70608/71. (9): *L. opalinum* β var. *subglabrum* [M], SMNS 70608/244. (13): *Bredya subinsignis* [?m], SMNS 70608/72. (14–17): *Pleurolytoceras dilucidum* [m], (14) SMNS 70608/73, (15) SMNS 70608/74, (16) SMNS 70608/75, (17) SMNS 70608/76. (2–17) eastern tributary of the Pliensbach creek at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, “Dilucidum-Schichten“, at a small waterfall (except Figs. 9a–b, 17: from a concretion layer c. 0.6 m below the bottom of the small waterfall). (2–17); Lower Aalenian, Opalinum Zone, Opalinum Subzone, *dilucidum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

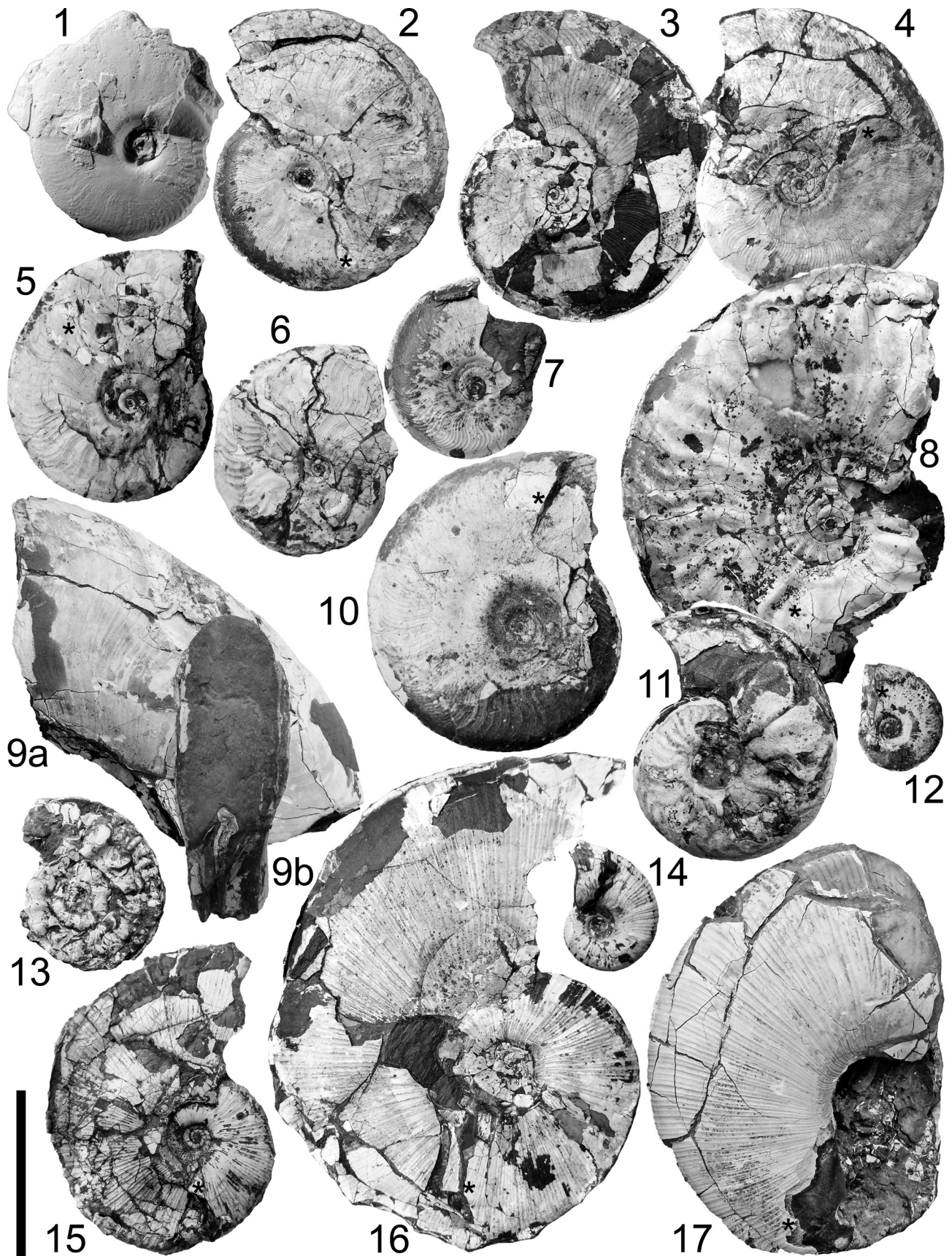


Plate 4

(1a): *Leioceras* ex gr. *opaliniforme* (BUCKMAN) [M], SMNS 70608/245. **(1b):** Nucleus of *Leioceras* sp. (1) SMNS 70608/77, Aichelberg slope of the motorway A8. **(2):** Pentacrinitenplatte with numerous disaggregated columnalia of *Chariocrinus wuerttembergicus* (OPPEL), small-sized *Scaphotrigonia navis* and bored pebbles, SMNS 70608/78 [leg. K.-H. VEIT], Teufelsklingenbach creek at Bad Boll-Eckwälden. **(3):** *L.* ex gr. *opaliniforme* (BUCKMAN) [M], SMNS 70608/79. Teufelsklingenbach creek at Bad Boll-Eckwälden. (1–3) Opalinuston Formation, Teufelsloch Member, Level of the Pentacrinitenplatten; Lower Aalenian, Opalinum Zone, Opalinum Subzone, ?*opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm.

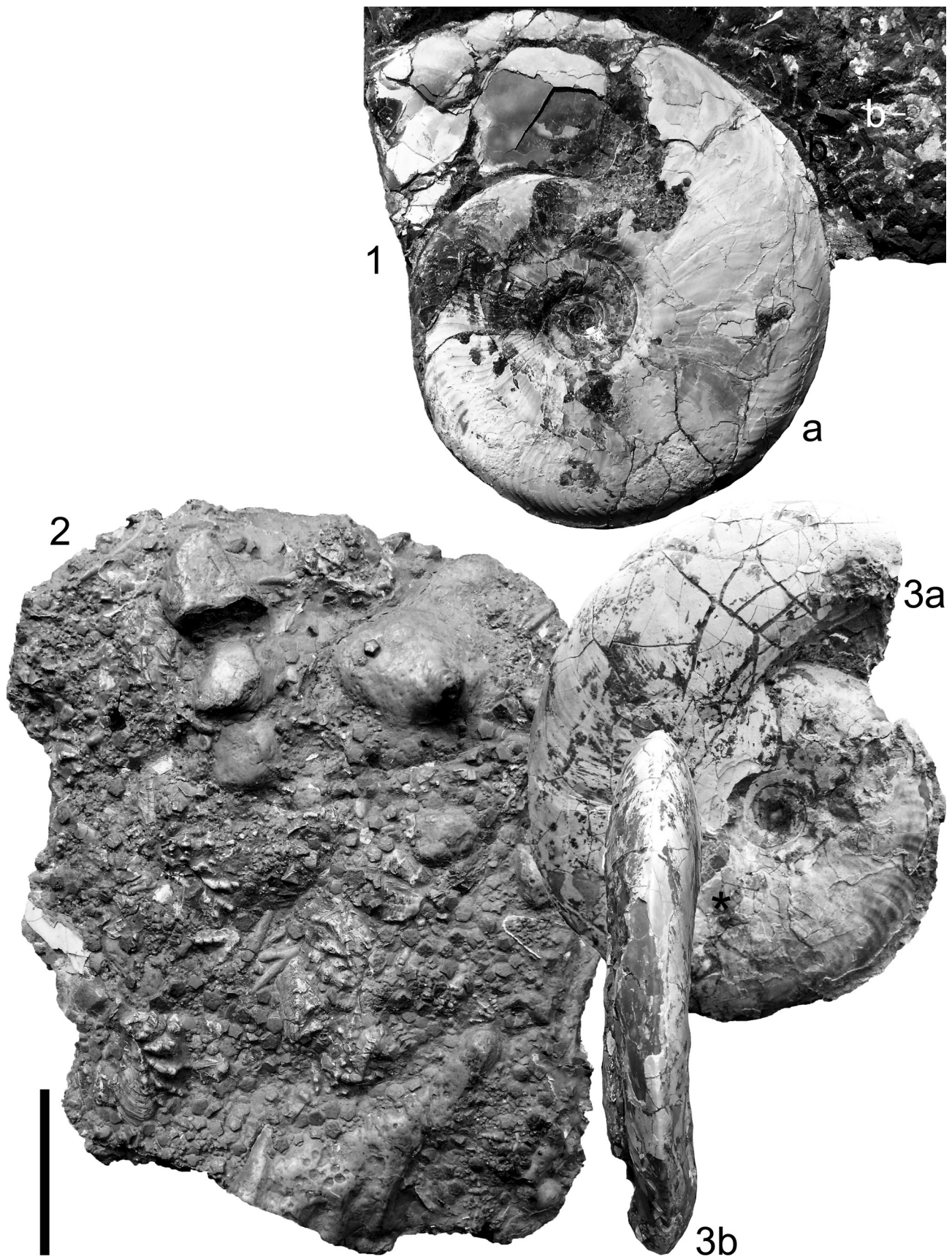


Plate 5

(1): *Leioceras opaliniforme* var. *opalinum* [m], SMNS 70608/80 (OpK IV), (2a, 4, 5, 7–9a, b, 12b): *L. opaliniforme* var. *partitum* [m], (2a) SMNS 70608/81 (OpK X), (4a–c) SMNS 70608/82, SMNS 70608/246, SMNS 70608/247 (OpK IX), (5) SMNS 70608/83 (OpK I), (7) SMNS 70608/248 (OpK IX), (8) SMNS 70608/249 (OpK VI), (9a, b) SMNS 70608/84, SMNS 70608/250 (OpK I), (12b) SMNS 70608/85 (OpK IX). (2b, c, 11): *L. hansrieberi* var. *comatum* [m], (2b, c) SMNS 70608/251, SMNS 70608/252 (OpK X), (11) SMNS 70608/86 (OpK I). (3, 6): *L. opaliniforme* [m], (3) SMNS 70608/87 (OpK IV), (6) SMNS 70608/88 (OpK I). (10) *L. opaliniforme* [M], SMNS 70608/89 (OpK VI). (12a) *L. opaliniforme* var. *subcostosum* [m], SMNS 70608/253 (OpK IX). (1–12) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Teufelsloch Member, Opaliniforme-Schichten [(1–9, 11–12) bed K 10; (10) bed K 13]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

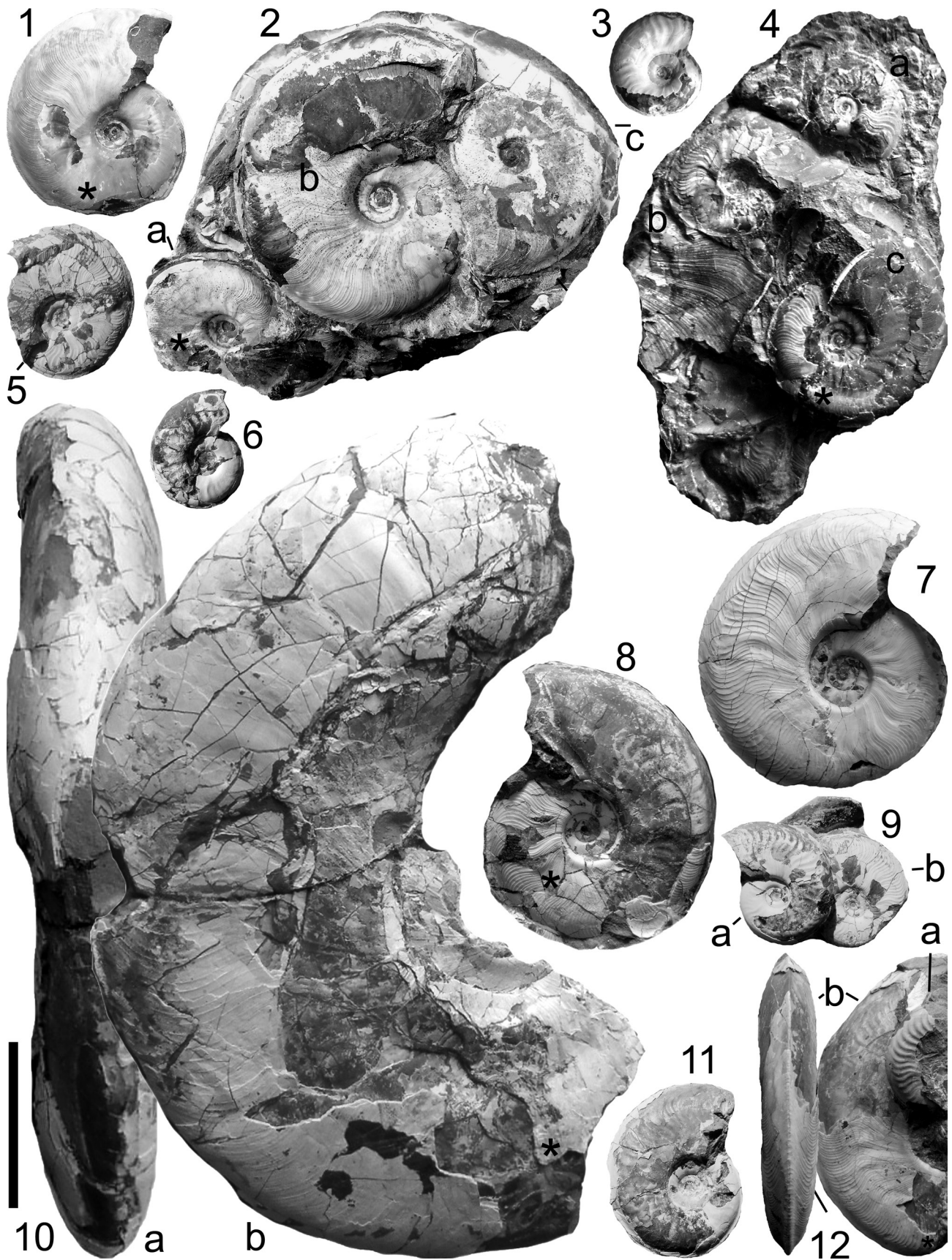


Plate 6

(1, 2b, 3–5, 7, 9, 10, 11a, c): *Leioceras opaliniforme* var. *partitum* [m], (1) SMNS 70608/90 (OpK IX), (2b) SMNS 70608/91 (OpK I), (3a, b) SMNS 70608/92, SMNS 70608/254 (OpK X), (4) SMNS 70608/93 (OpK IX), (5) SMNS 70608/94 (OpK I), (7) SMNS 70608/95 (OpK II), (9) SMNS 70608/96 (OpK I), (10a, b) SMNS 70608/97, SMNS 70608/255 (OpK IX), (11a) SMNS 70608/256 (OpK I), (11c) SMNS 70608/257 (OpK I). (2a, 11d–f): *L. opaliniforme* var. *tyrrhenum* [M] (2a, 11d–f) SMNS 70608/258, SMNS 70608/259, SMNS 70608/260, SMNS 70608/261 (OpK I). (6, 13, 14): *L. hansrieberi* var. *subcostosum* [m], (6) SMNS 70608/98 (OpK IX), (13) SMNS 70608/99 (OpK IX), (14) LGRB/E 848. (8, 11b) *L. hansrieberi* [m], SMNS 70608/100 (OpK I), SMNS 70608/262 (OpK I). (11b): *Leioceras* sp. [m], SMNS 70608/263 (OpK I). (12a, b): *L. opaliniforme* var. *comatum* [m], SMNS 70608/101, SMNS 70608/264 (OpK VIII). (1–14) Teufelsklängenbach creek at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, Opaliniforme-Schichten [bed K 10]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

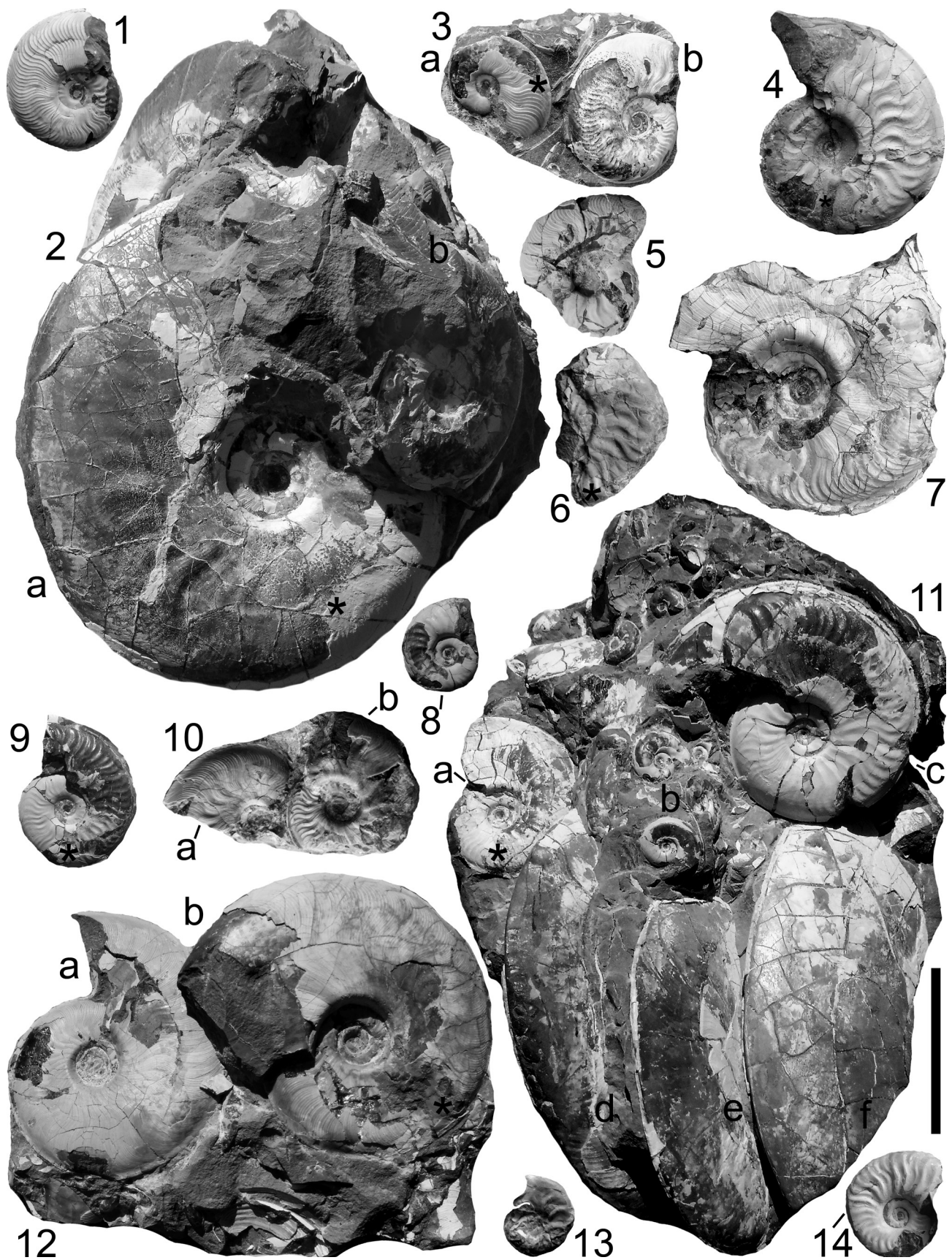


Plate 7

(**1, 2**): *Leioceras opaliniforme* [M], (1) SMNS 70608/102, (2) SMNS 70608/103. (**3**) *Leioceras opaliniforme* var. *hansrieberi* [M], SMNS 70608/104. (1–3) Teufelsklingenbach creek at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, Opaliniforme-Schichten [bed K 10; claystone]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

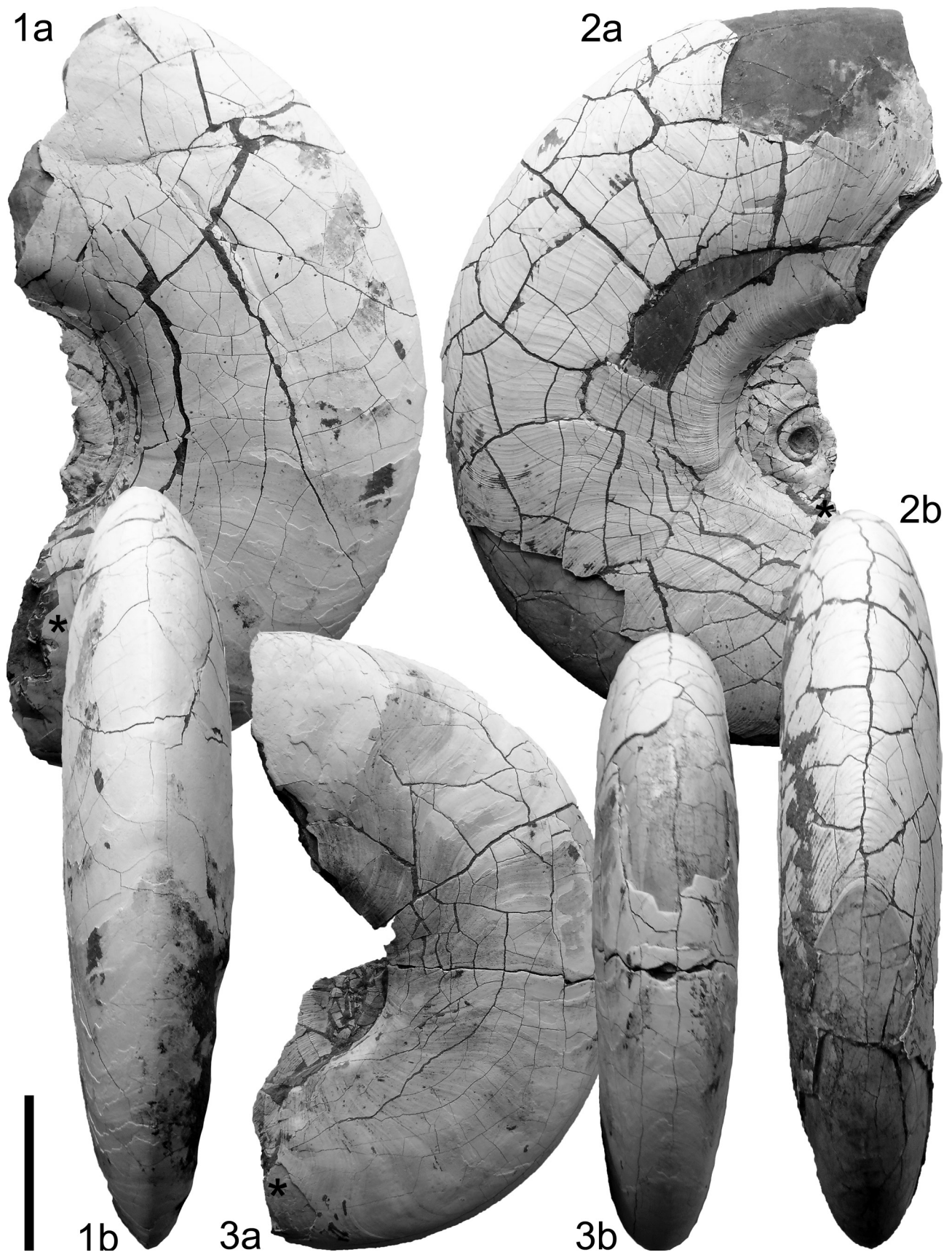


Plate 8

(1a, b): *Leioceras opaliniforme* var. *hansrieberi* [M], juvenile, SMNS 70608/105. (2, 3): *L. opaliniforme* [M], juvenile, (2) SMNS 70608/106, (3) SMNS 70608/107. (4, 5) *Pleurolytoceras dilucidum*, (4) SMNS 70608/108, (5) SMNS 70608/109. (1–5) Teufelsklingenbach creek at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, Opaliniforme-Schichten [bed K 10, Tonstein]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

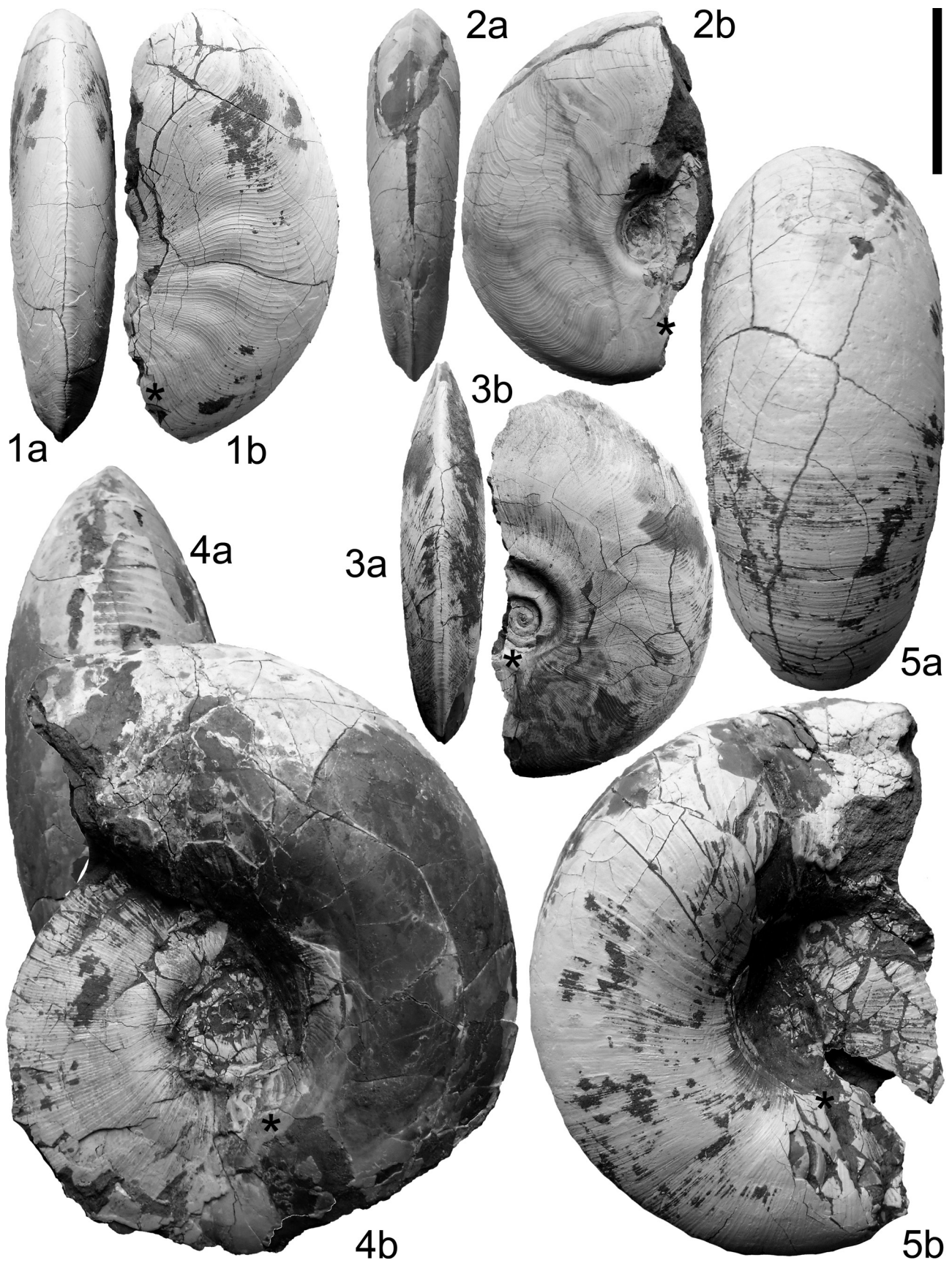


Plate 9

(1, 2, 7): *Leioceras opaliniforme* [M], (1) SMNS 70608/110, (2) SMNS 70608/111, juvenile, (7) SMNS 70608/112. **(3–5):** *L. opaliniforme* [?M], nuclei of juveniles, (3) SMNS 70608/113, (4) SMNS 70608/114, (5) SMNS 70608/115. **(6)** *L. opaliniforme* [m], SMNS 70608/116. (1–7) Teufelsklingenbach creek at Bad Boll-Eckwälden. Opalinuston Formation, Teufelsloch Member, Opaliniforme-Schichten [(2–7) bed K 13, claystone; (1) bed K 10, “Opalinusknolle”]; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *opaliniforme* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

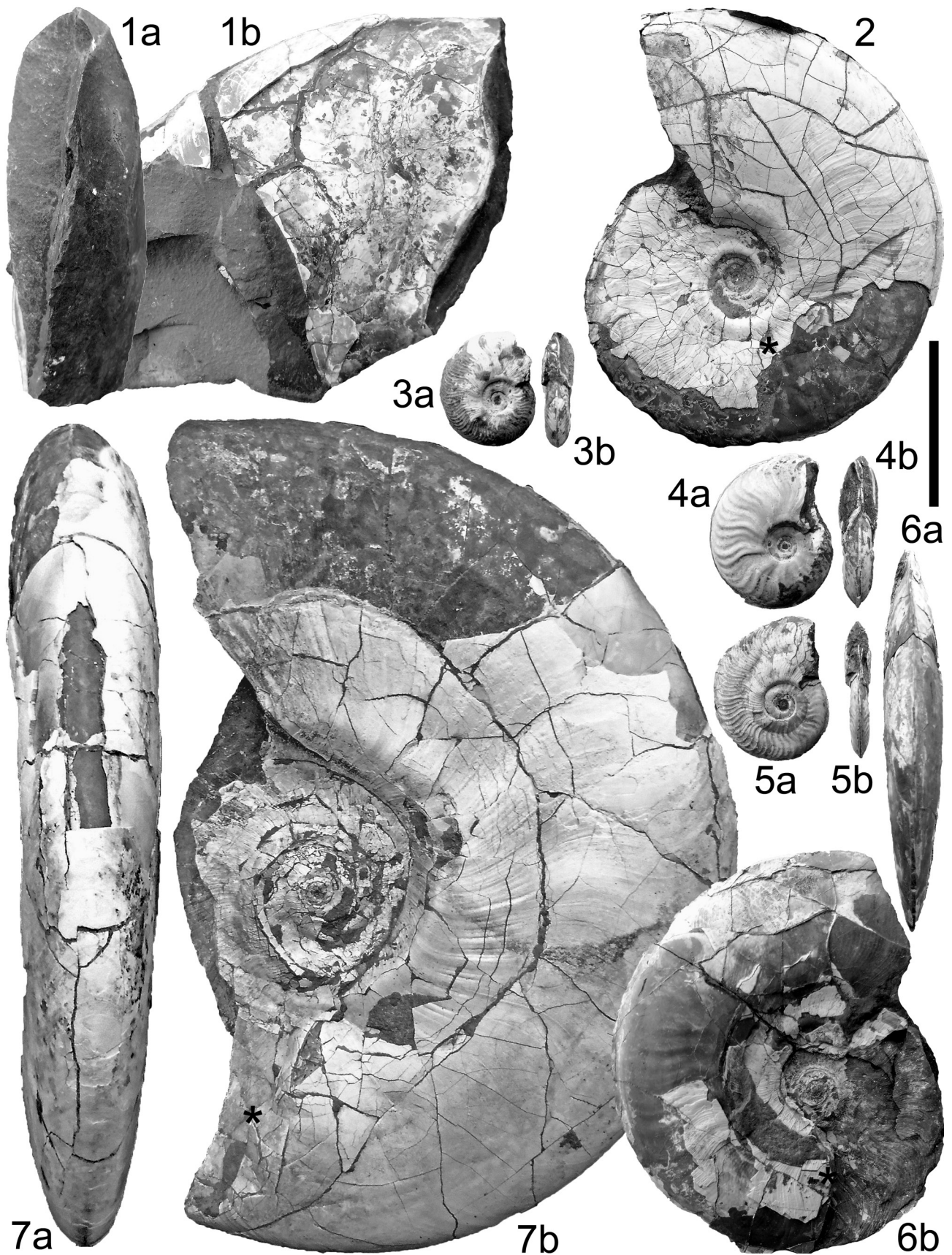


Plate 10

(1, 4, 6, 7a, b): *Leioceras hansrieberi* var. *subcostosum* [m], (1) SMNS 70608/265 (OpK “B”), (4) SMNS 70608/266 (OpK “C”), (6) SMNS 70608/267 (OpK “B”), (7a, b) SMNS 70608/268 (OpK “A”). (2, 3, 5, 7d, e): *L. hansrieberi* var. *partitum* [m], (2) SMNS 70608/269 (OpK “A”), (3) SMNS 70608/270 (OpK “C”), (5) SMNS 70608/271 (OpK “C”), (7d, e) SMNS 70608/272, SMNS 70608/273, (OpK “A”). (7c) *L. hansrieberi* [M], SMNS 70608/274 (OpK “A”). (1–6) Teufelsklingenbach creek at Bad Boll-Eckwälden. (7) Riesbach creek at Bad Boll (1–7) Opalinuston Formation, Teufelsloch Member, Wasserfallschichten, c. 6.5 m below top Wasserfallbank; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

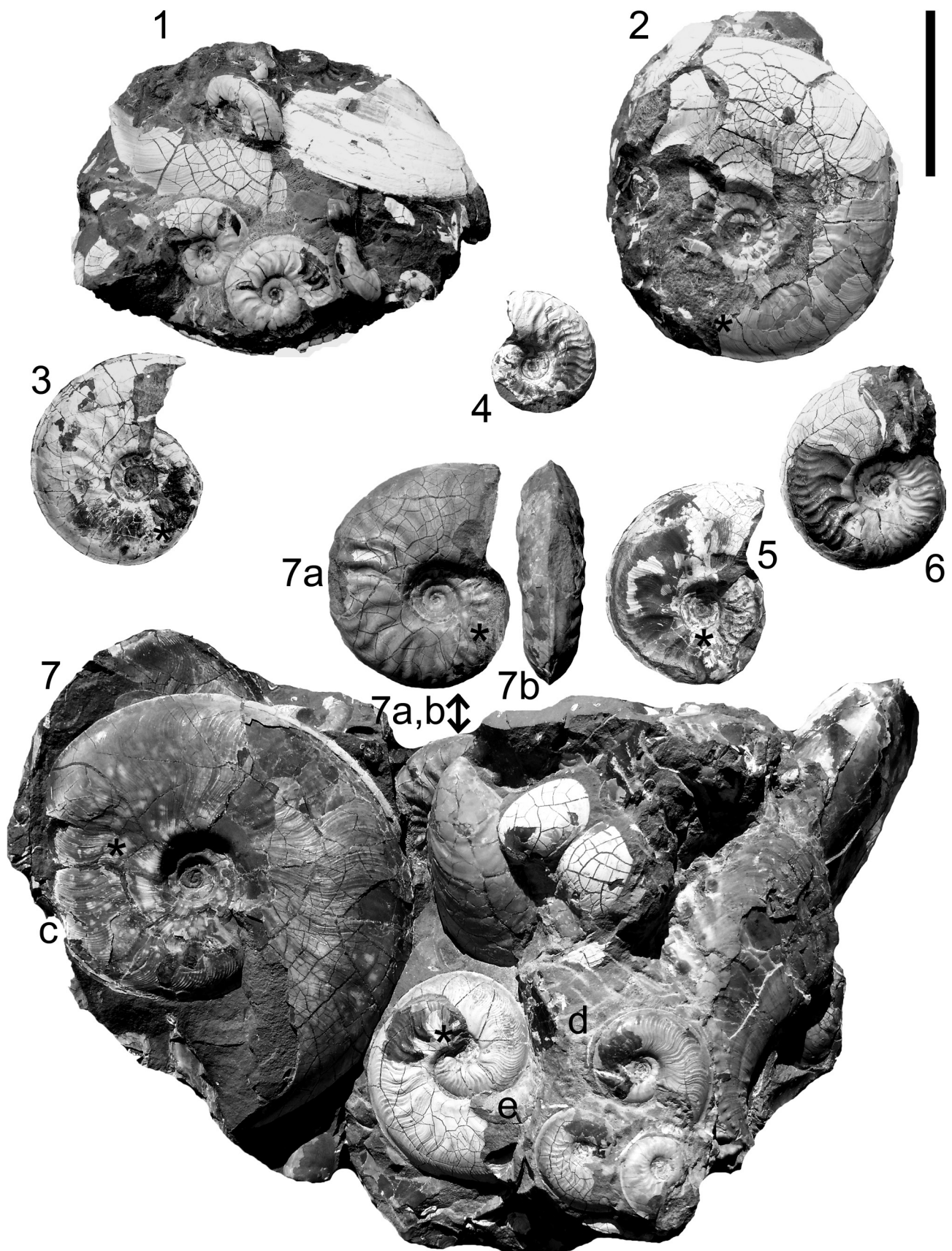


Plate 11

(1–3): *Leioceras hansrieberi* [M], (1) SMNS 70608/275. (2) SMNS 70608/276, juvenile, (3) SMNS 70608/277, juvenile. (1–3) Teufelsklungenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, Wasserfallschichten (c. 5.2 m below top Wasserfallbank); Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

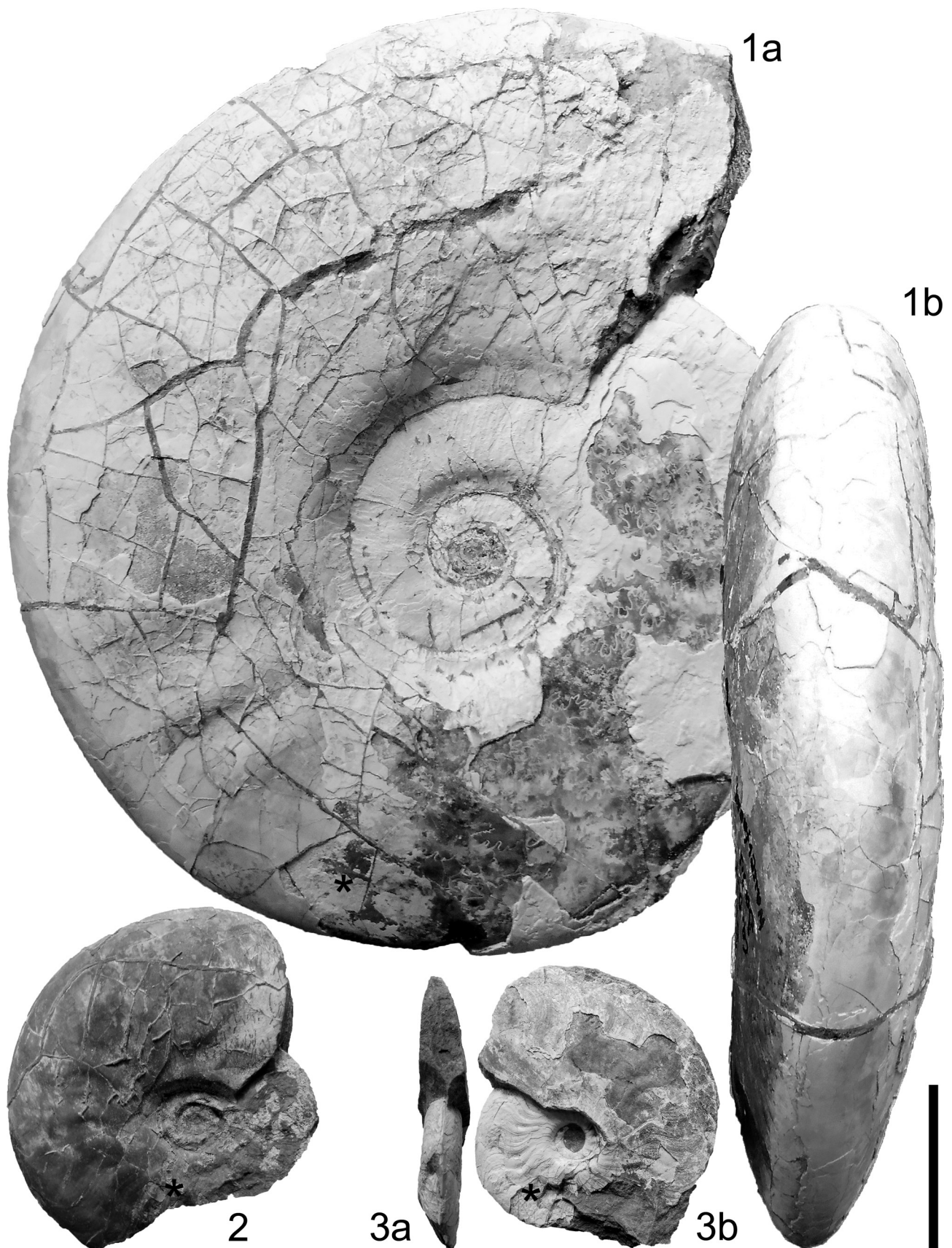


Plate 12

(1, 2): *Leioceras hansrieberi* [M], (1) SMNS 70608/278, juvenile, (2) SMNS 70608/279, Riesbach creek at Bad Boll, c. 6.8 m below top Wasserfallbank. **(3–5)** *L. hansrieberi* [?m], (3) SMNS 70608/117, (4) SMNS 70608/118, (5) SMNS 70608/119. (1, 3–5) Teufelsklingenbach creek at Bad Boll-Eckwälden, c. 5 m below top Wasserfallbank; (1–5) Opalinuston Formation, Zillhausen Member, Wasserfallschichten; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

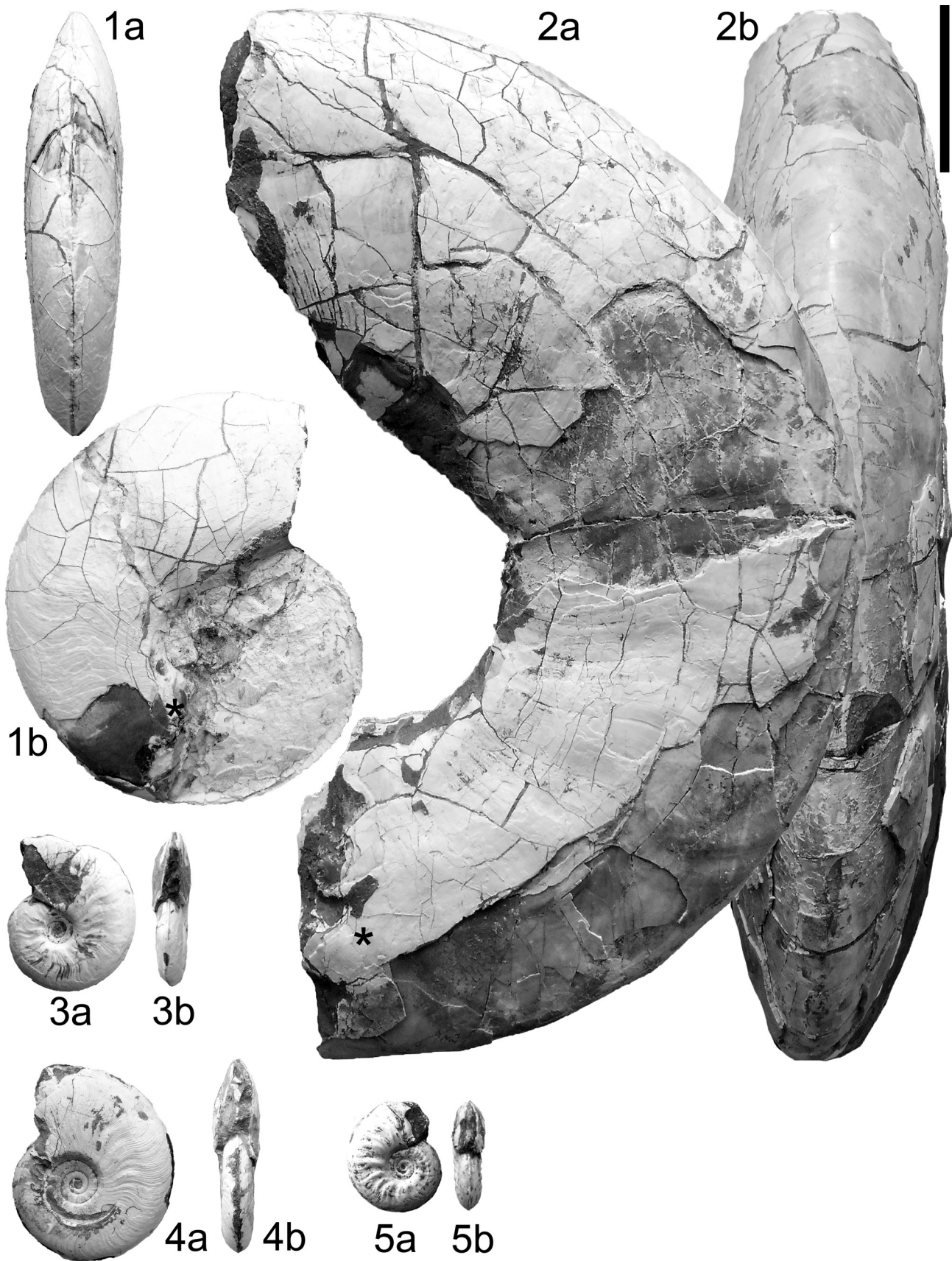


Plate 13

(1): *Leioceras hansrieberi* [M], SMNS 70608/120, Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, Wasserfallschichten (c. 5 m below top Wasserfallbank); Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonite at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

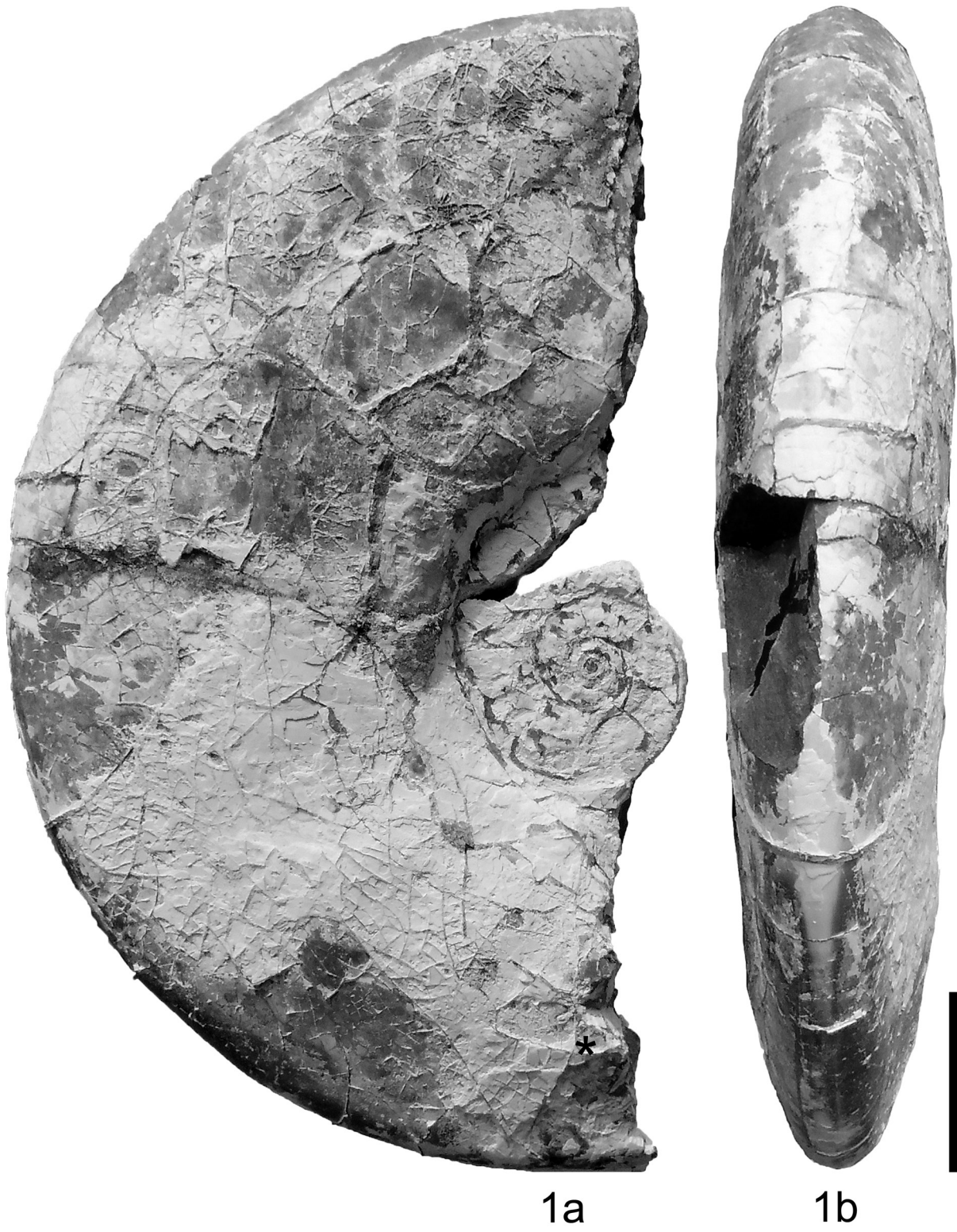


Plate 14

(1): *Leioceras hansrieberi* [M], SMNS 70608/121. (2–4) *L. hansrieberi* var. *partitum* [m]; (2) SMNS 70608/122, (3) SMNS 70608/123, (4) SMNS 70608/124. (1–4) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, Wasserfallschichten (c. 4.7 m below top Wasserfallbank); Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites in natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

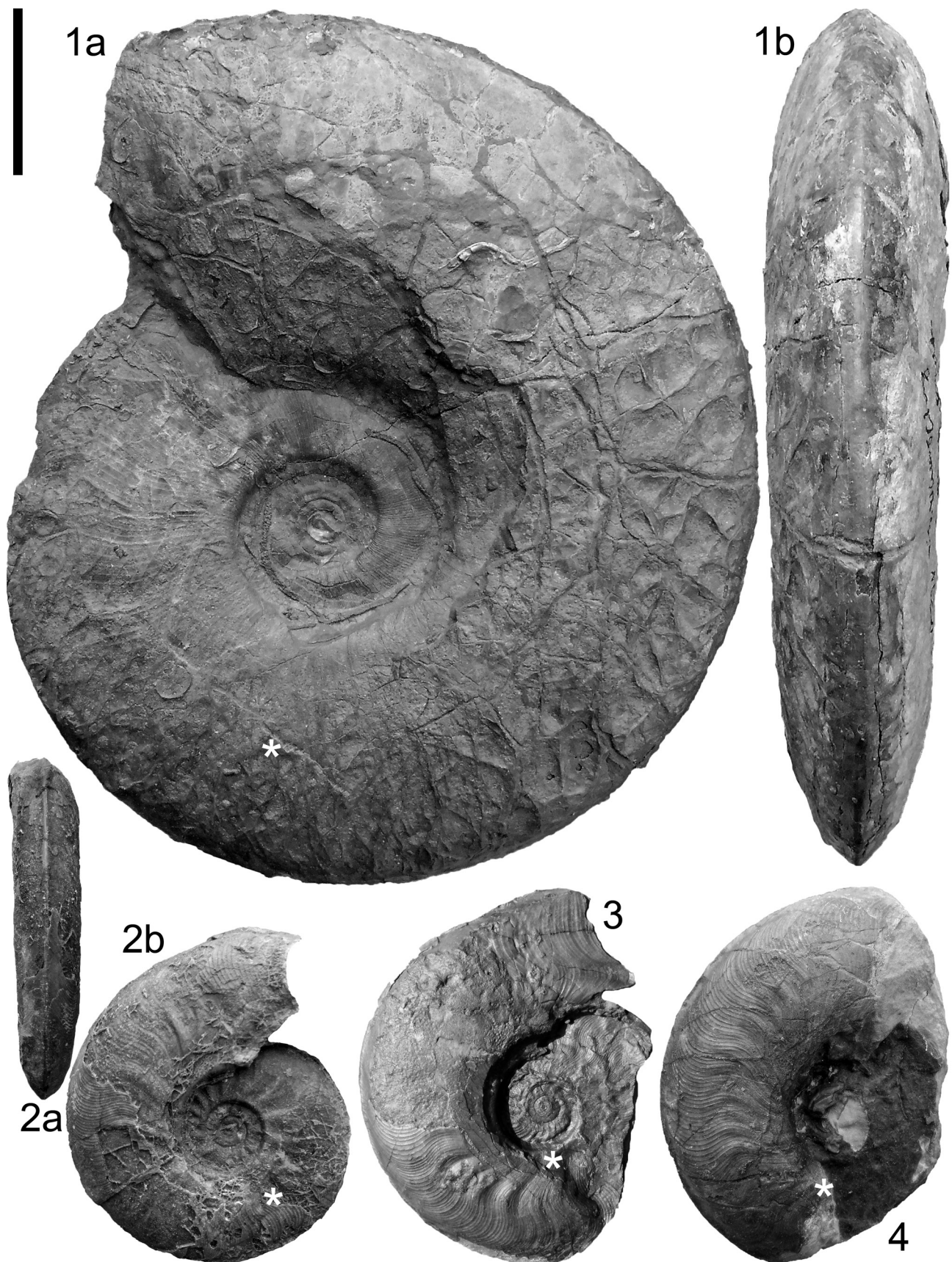


Plate 15

(1, 2): *Leioceras hansrieberi* [M], (1) SMNS 70608/125 (c. 3.9 m below top Wasserfallbank), (2) SMNS 70608/126 (c. 3.2 m below top Wasserfallbank). **(3)** *Tmetoceras scissum* [M], SMNS 70608/127 (c. 4.7 below top Wasserfallbank). (1–3) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, Wasserfallschichten; Lower Aalenian Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

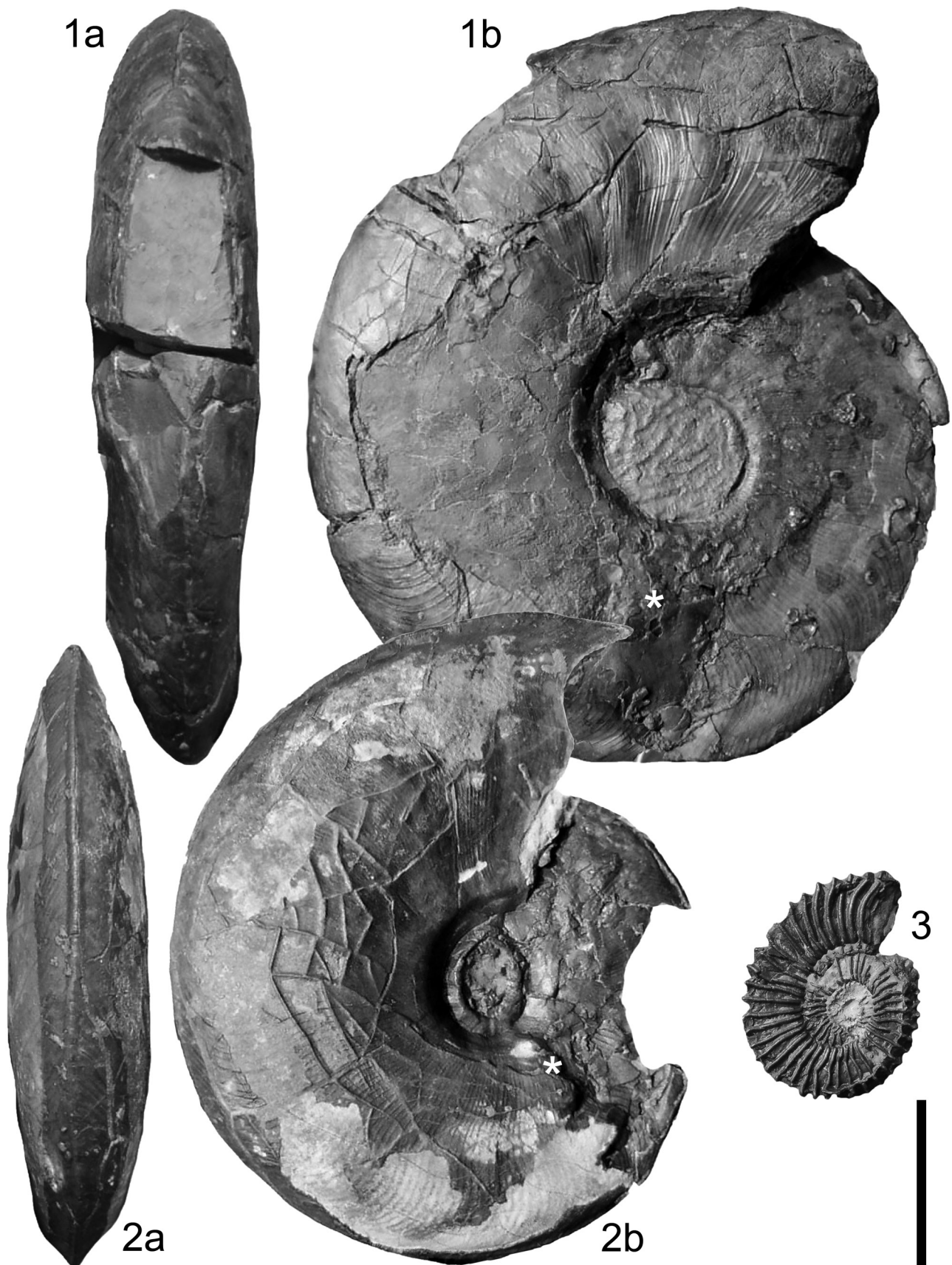


Plate 16

(1–4): *Leioceras hansrieberi* [M], (1) LGRB/E 847 (Wasserfallschichten, c. 1.2 m below top Wasserfallbank), (2) SMNS 70608/129 (Op 2, c. 0.2 above top Wasserfallbank). (3) SMNS 70608/130 (Op 2, c. 0.3 above top Wasserfallbank). (4) SMNS 70608/131 (Op 2, c. 2.0 m above top Wasserfallbank). (1–4) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member; Unter Aalenium, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.



Plate 17

(1): *Leioceras hansrieberi* [M], SMNS 70608/132 (Op 2, c. 2 m above top Wasserfallbank). Riesbach creek at Bad Boll; Achdorf Formation; Lower Aalenian, Opalinum Zone, Opalinum Subzone, *hansrieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.



Plate 18

(1): *Leioceras bifidatum* var. *rieberi* [M], SMNS 70608/133. (2) *L. bifidatum* var. aff. *rieberi* [M], Riesbach, SMNS 70608/134. (3–5): *L. bifidatum* var. *partitum* [m], (3) SMNS 70608/135, (4) SMNS 70608/136, (5) SMNS 70608/137. (6, 8–10) *L. bifidatum* var. cf. *crassicostatum* [M], (6) SMNS 70608/138, (8) SMNS 70608/139, (9) SMNS 70608/140, (10) SMNS 70608/141. (7): *L. bifidatum* var. *uncinatum* [M] SMNS 70608/142. (1, 3–10) Teufelsklängenbach creek at Bad Boll-Eckwälden. (1–10) Opalinuston Formation, Bifidatumbank (1–5: bed BB-1; 6–10: bed BB-2); Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *bifidatum/rieberi*-Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

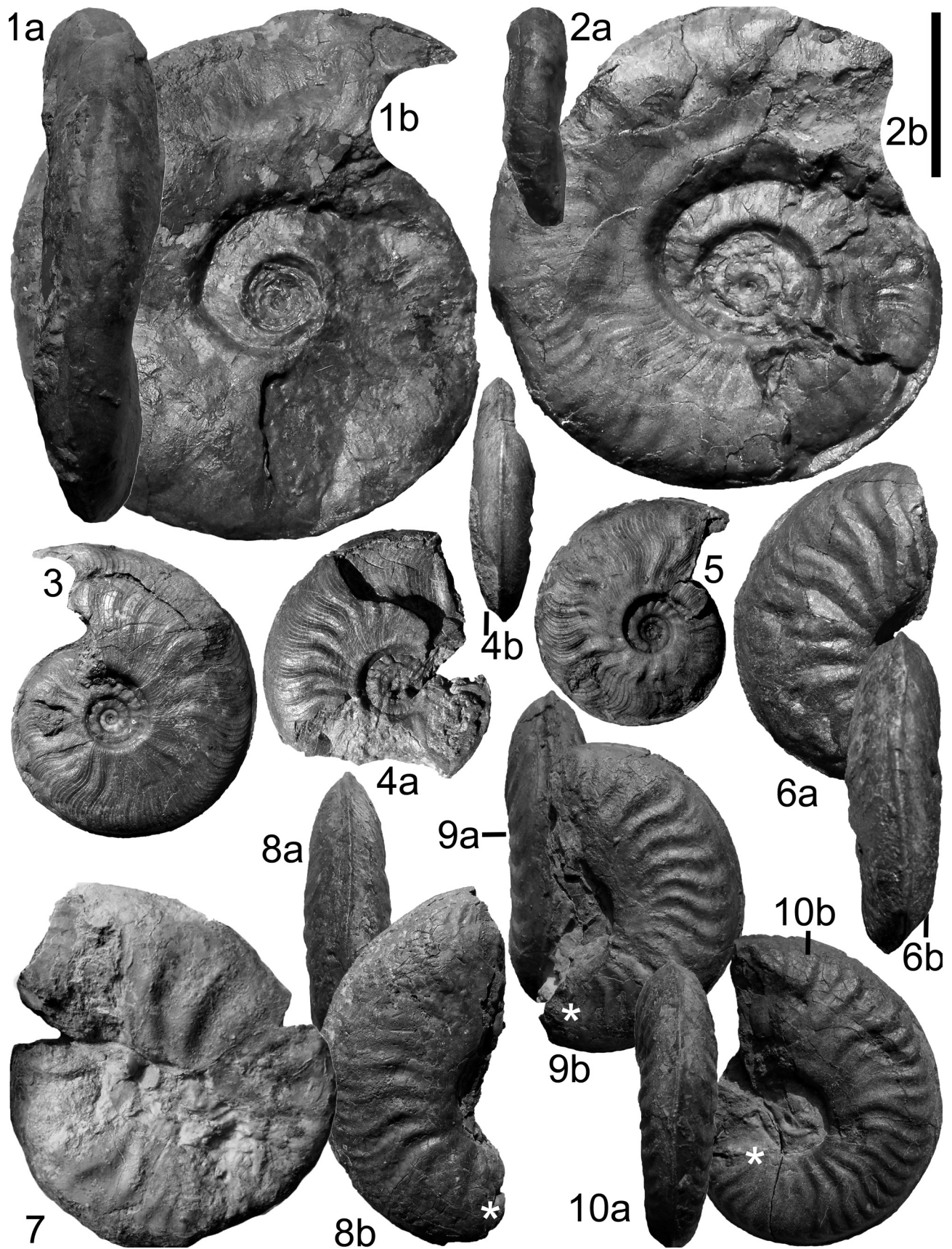


Plate 19

(1, 2): *Leioceras bifidatum* var. *rieberi* [M], (1) SMNS 70608/143, (2) SMNS 70608/144. **(3, 6)** *L. bifidatum* var. *plicatellum* [M], (3) SMNS 70608/145, (6) LGRB/E 849. **(4):** *L. bifidatum* [M], SMNS 70608/147. **(5):** *L. bifidatum* var. *spathi* [M], SMNS 70608/148. (1a–6b) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Bifidatumbank, bed BB-2; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *bifidatum/rieberi*-Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

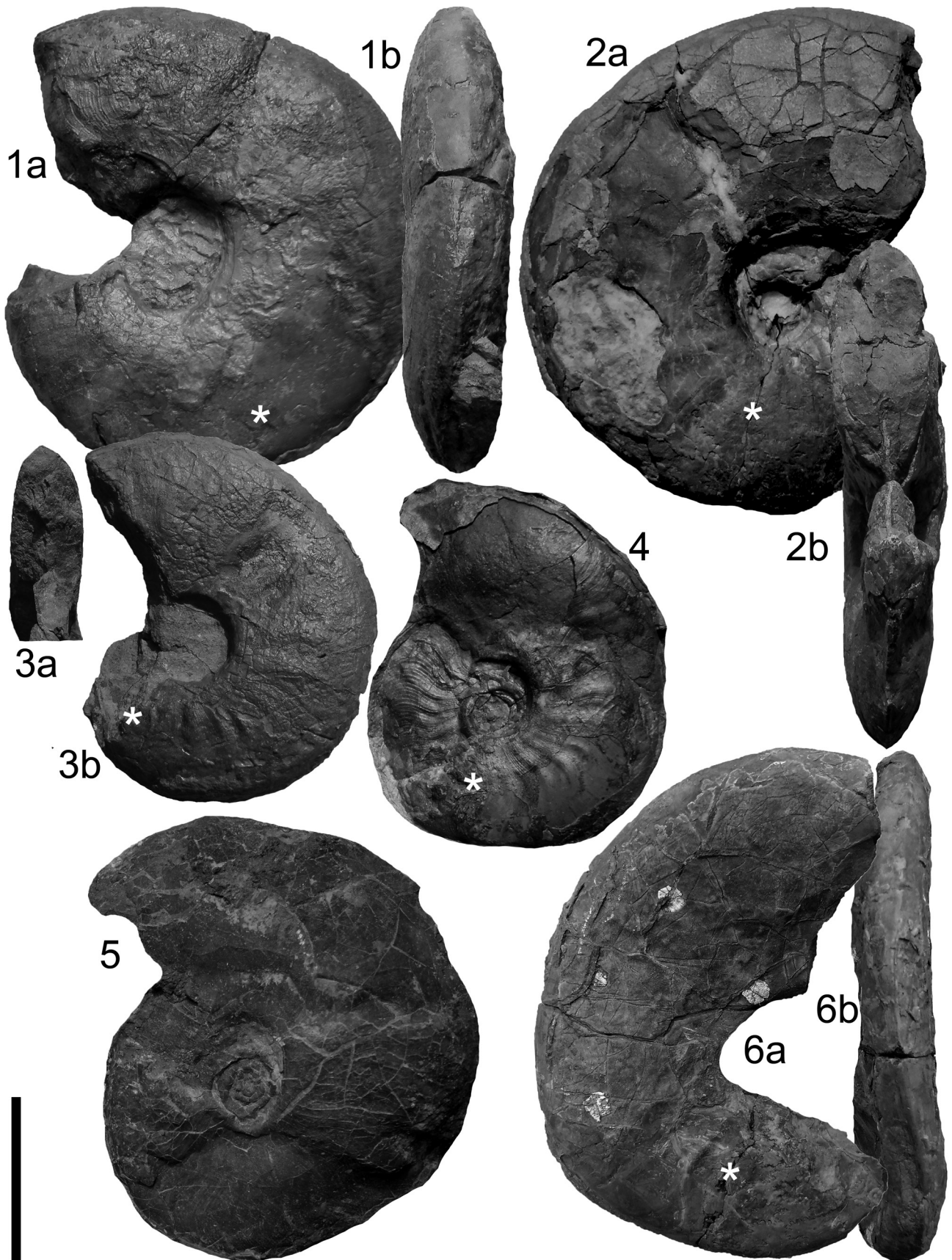


Plate 20

(1–7): *Leioceras bifidatum* var. *striatum* [m], (1) SMNS 70608/149, (2) SMNS 70608/150, (3) SMNS 70608/151, (4) SMNS 70608/152, (5) LGRB/E 850, (6) SMNS 70608/154, (7) SMNS 70608/155. (8, 11, 12): *L. bifidatum* var. aff. *striatum* [m], (8) SMNS 70608/156, (11) SMNS 70608/157, (12) SMNS 70608/158. (9, 10): *L. bifidatum* var. *partitum* [m], (9) SMNS 70608/280, (10) SMNS 70608/146. (13–15): *L. bifidatum* var. aff. *subcostosum* [m], (13) SMNS 70608/281, (14) SMNS 70608/159, (15a, b) SMNS 70608/160, SMNS 70608/282. (16): *L. bifidatum* var. *paucicostatum* [m] SMNS 70608/283. (1–16) Teufelsklingsbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Bifidatumbank, bed BB-2; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *bifidatum/rieberi* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

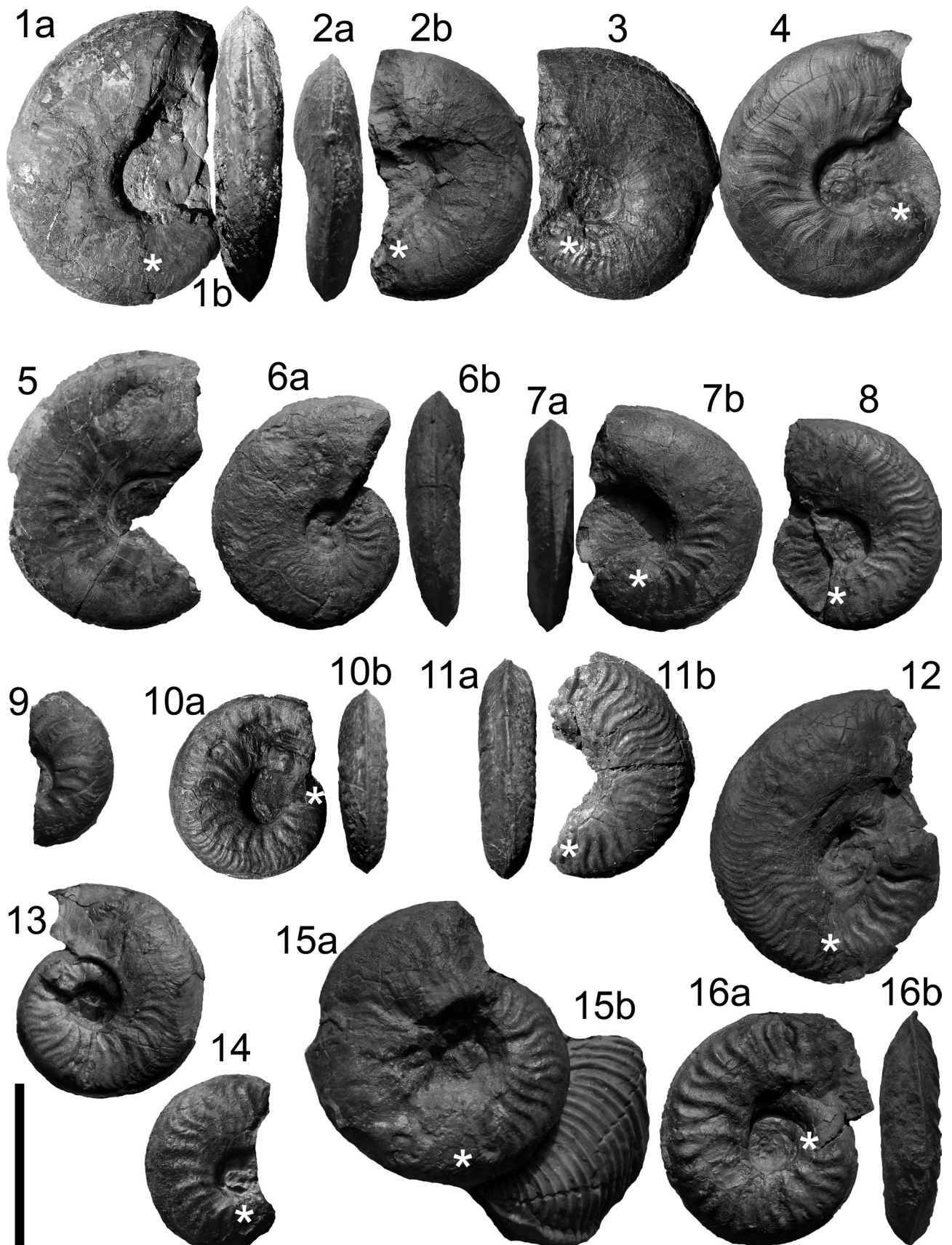


Plate 21

(1–4): *Leioceras uncinatum* [M], (1) SMNS 70608/161, (2) SMNS 70608/162, (3) SMNS 70608/163, (4) SMNS 70608/164. (5): *L. uncinatum* var. *stephanovi* [M], SMNS 70608/165. (1–5) Teufelsklingsbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, level of the ‘Zopfplatten’, ZoP 5; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *uncinatum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

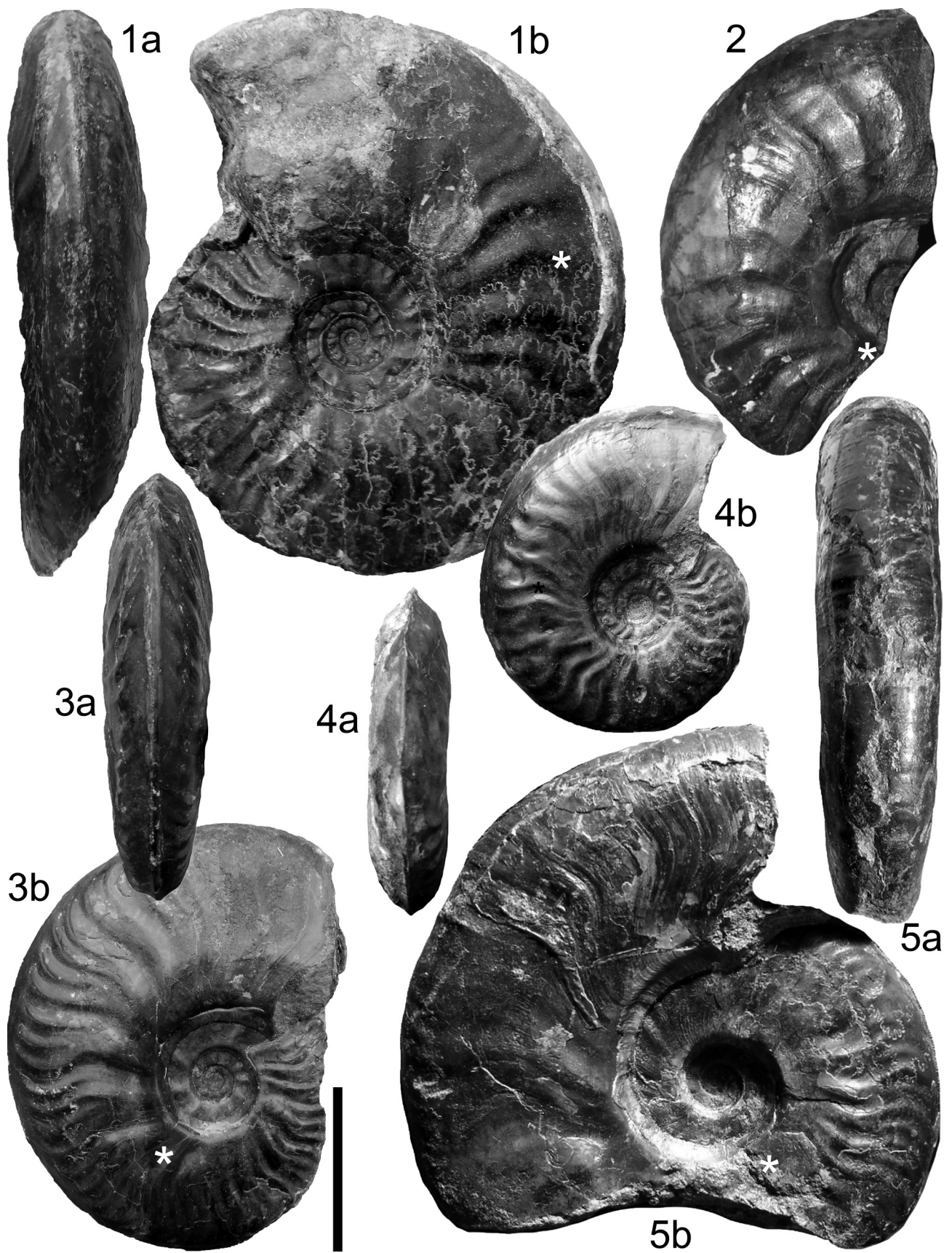


Plate 22

(1, 2): *Leioceras uncinatum* var. *bifidatum* [M], (1) SMNS 70608/166, (2) SMNS 70608/167. **(3, 4, 7, 8a, 8e):** *L. uncinatum* var. *plicatellum* [M], (3) SMNS 70608/168, (4) SMNS 70608/169, (7) SMNS 70608/170, (8a, e) SMNS 70608/171, SMNS 70608/284. **(5):** *L. uncinatum* var. *plectile* [M], SMNS 70608/172. **(6):** *L. uncinatum* var. *stephanovi* [M], SMNS 70608/153. **(8b):** *L. uncinatum* var. *striatum* [m], SMNS 70608/285. **(8c, d):** *L. uncinatum* var. *subcostosum* [m], SMNS 70608/286, 70608/287. (1–8) Teufelsklingsbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, level of the ‘Zopfplatten’, ZoP 5; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *uncinatum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

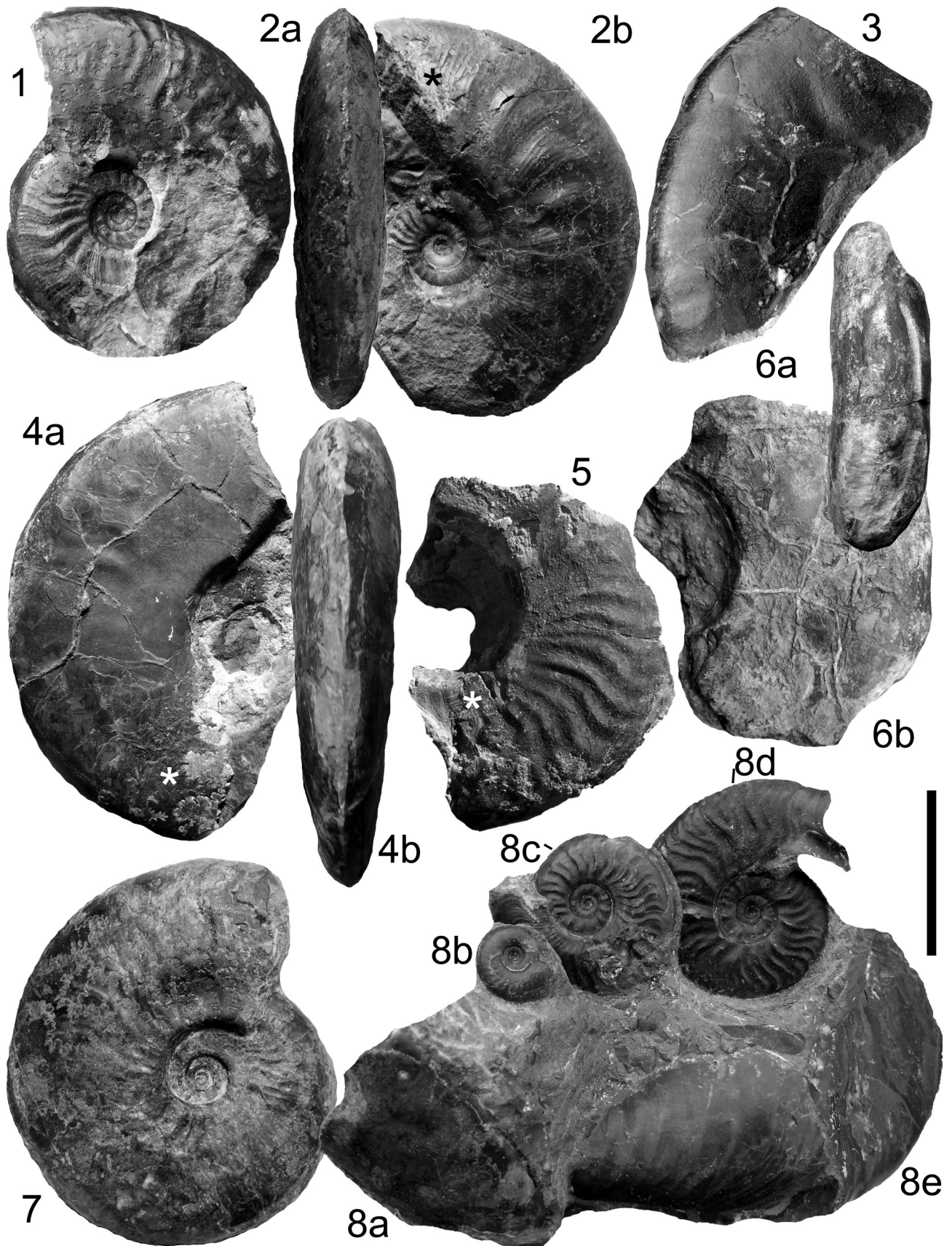


Plate 23

(**1, 2, 5–8**): *Leioceras uncinatum* var. *paucicostatum* [m], (1) SMNS 70608/173, (2) SMNS 70608/174, (5) SMNS 70608/175, (6) SMNS 70608/176, (7) SMNS 70608/177, (8) SMNS 70608/178. (**3, 4, 9, 13, 18**): *L. uncinatum* var. *subcostosum* [m], (3) SMNS 70608/179, (4) SMNS 70608/180, (9) SMNS 70608/181, (13) SMNS 70608/182, (18) SMNS 70608/183. (**10–12, 14, 15**): *L. uncinatum* var. *partitum* [m], (10) SMNS 70608/184, (11) SMNS 70608/185, (12) SMNS 70608/186, (14) SMNS 70608/187, (15) SMNS 70608/188. (**16, 17, 19–23**): *L. uncinatum* var. *striatum* [m], (16) SMNS 70608/189, (17) SMNS 70608/190, (19) SMNS 70608/191, (20) SMNS 70608/192, (21) SMNS 70608/193, (22) SMNS 70608/194, (23) SMNS 70608/195. (1–23) Teufelsklingenbach creek at Bad Boll-Eckwälden; Opalinuston Formation, Zillhausen Member, level of the ‘Zopfplatten’, ZoP 5 (except Figs. 8, 12, 13 = ZoP 6); Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *uncinatum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

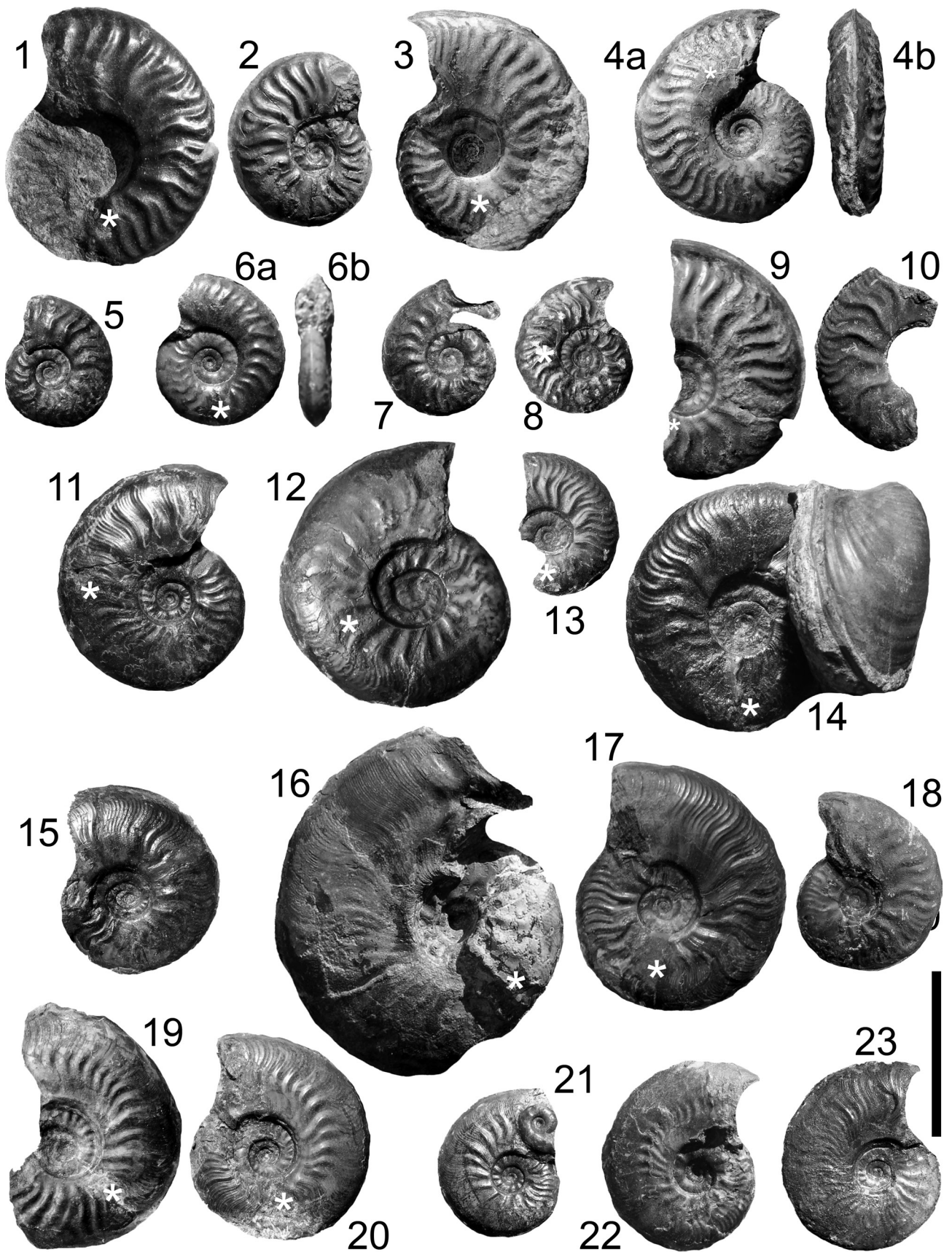


Plate 24

(1): *Leioceras evolutum* var. *comptocostosum* [M], SMNS 70608/196. (2, 3): *L. evolutum* var. *crassicostatum* [M], (2) SMNS 70608/197, (3) SMNS 70608/198. (4): *L. evolutum* var. *costate* sensu CONTINI [M], SMNS 70608/199. (5): *L. evolutum* var. *subcostate* sensu CONTINI [M], SMNS 70608/200. (6–8): *L. evolutum* var. *striate* sensu CONTINI [M] (6) SMNS 70608/201, (7) SMNS 70608/202, (8) SMNS 70608/203. (1–8) Teufelsklängenbach creek at Bad Boll-Eckwälden; Achdorf Formation, Wilflingen-Bank; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *evolutum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

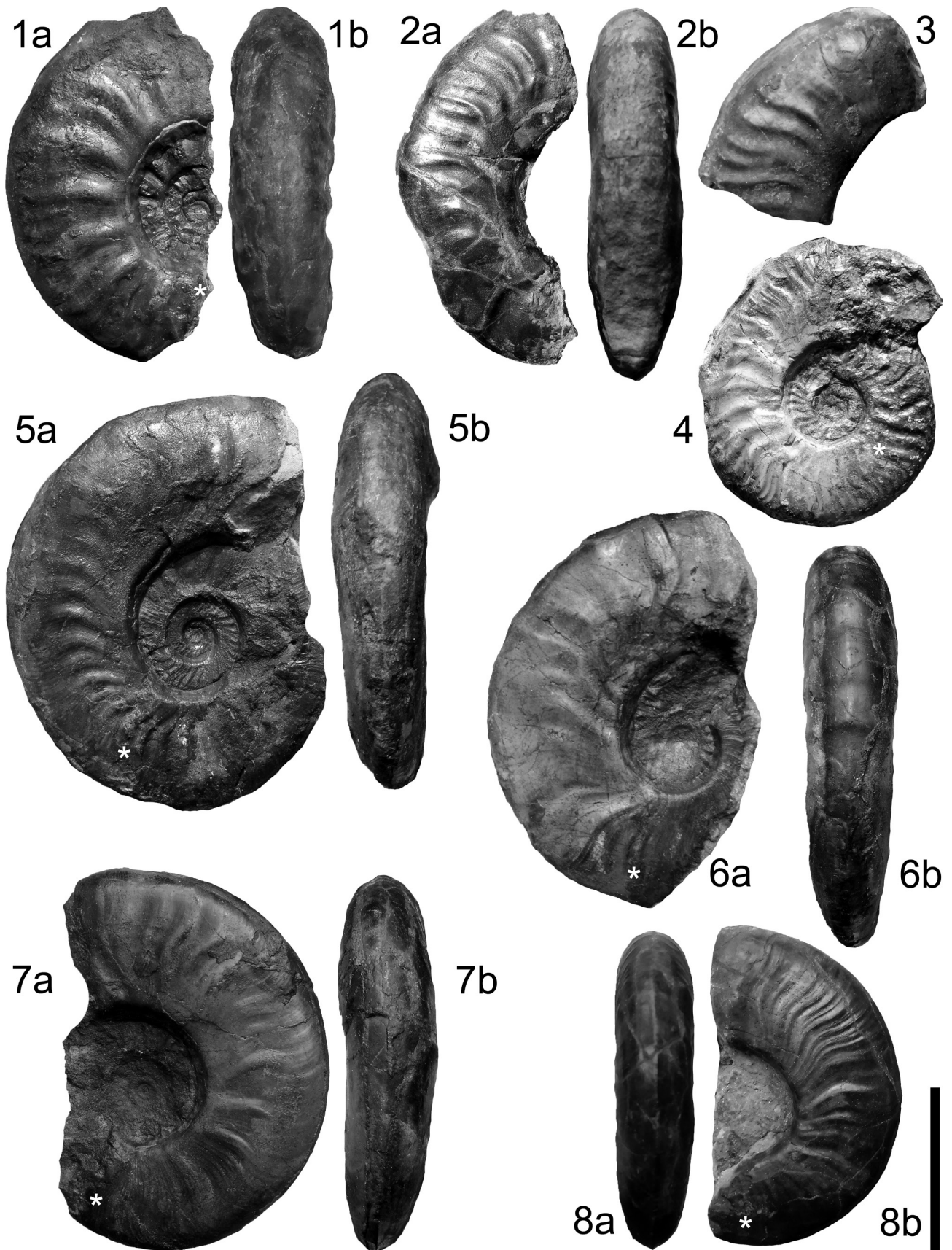


Plate 25

(1, 3a): *Leioceras evolutum* var. *costate* sensu CONTINI [M], (1) SMNS 70608/204, (3a) LGRB/E 853. (2, 3b, c, 4, 5): *L. evolutum* var. *striate* sensu CONTINI [M], (2) LGRB 70608/70608, (3b, c) LGRB/E 852, (4) SMNS 70608/205, (5) SMNS 70608/206. (6a, b, 7, 8, 13–18, 23a): *L. evolutum* var. *paucicostatum* [m]; (6a) SMNS 70608/208, (6b) SMNS 70608/288, (7) LGRB/E 854, (8) SMNS 70608/210, (13) SMNS 70608/211, (14) SMNS 70608/212, (15) SMNS 70608/213, (16) SMNS 70608/214, (17) SMNS 70608/215, (18) SMNS 70608/216, (23a) SMNS 70608/217. (9–12, 19–22, 23b–25): *L. evolutum* var. *striatum* [m]; (9) SMNS 70608/218, (10) SMNS 70608/219, (11) SMNS 70608/220, (12) SMNS 70608/221, (19) SMNS 70608/222, (20) SMNS 70608/223, (21) SMNS 70608/224, (22) SMNS 70608/225, (23b) SMNS 70608/226, (24) SMNS 70608/227, (25) SMNS 70608/228. (1–12) Teufelsklingsbach creek at Bad Boll-Eckwälden; (13–25) ‘Grünbrücke’ at motorway A8 at Aichelberg slope. (1–25) Achdorf Formation, Wilflingen-Bank; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *evolutum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

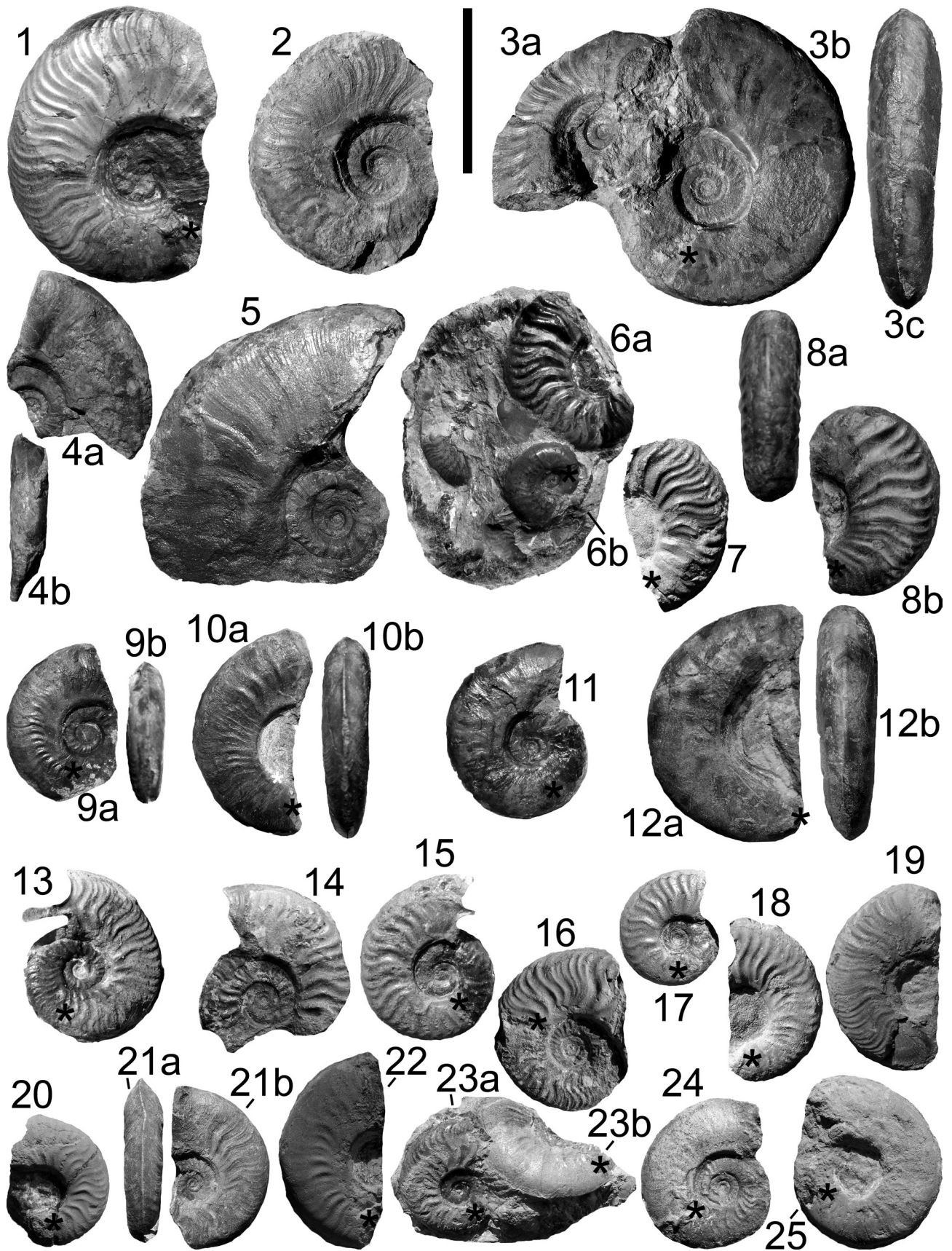


Plate 26

(1–3): *Leioceras evolutum* var. *costate* sensu CONTINI [M], (1) SMNS 70608/230, (2) SMNS 70608/231, (3) SMNS 70608/232.
(4–6): *L. evolutum* var. *subcostate* sensu CONTINI [M], (4) SMNS 70608/233, (5) SMNS 70608/234, (6) SMNS 70608/235.
(7–12): *L. evolutum* var. *striate* sensu CONTINI [M], (7) SMNS 70608/236, (8) SMNS 70608/237, (9) SMNS 70608/238, (10) SMNS 70608/239, (11) SMNS 70608/240, (12) SMNS 70608/241. (1–12) ‘Grünbrücke’ at the motorway A8 at Aichelberg slope; Achdorf Formation, Wilflingen-Bank; Lower Aalenian, Opalinum Zone, Bifidatum Subzone, *evolutum* Biohorizon. Ammonites at natural size. Scale bar equals 30 mm. The beginning of the body chamber is marked by an asterisk.

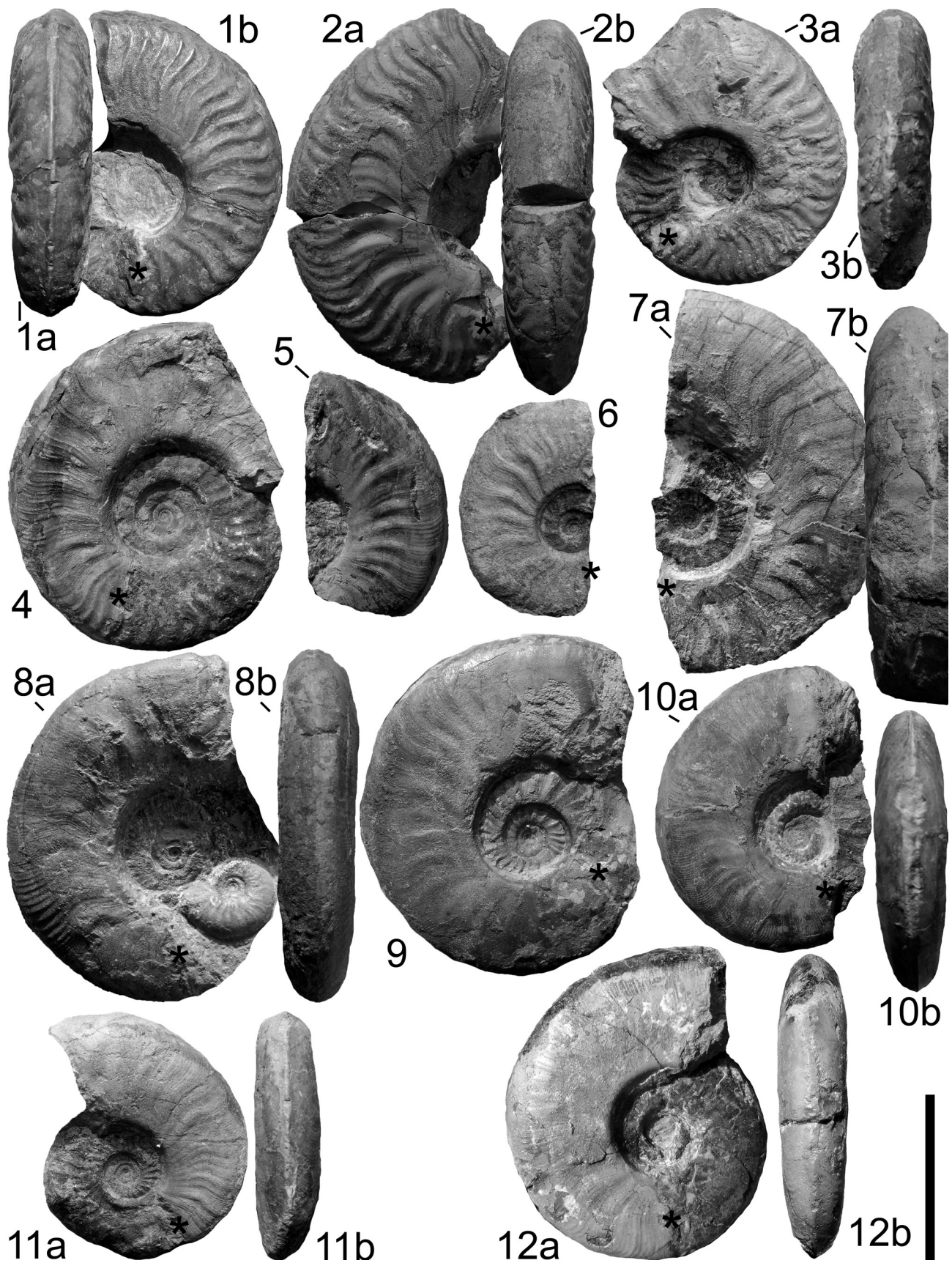


Plate 27

Additional invertebrate fauna of the Opalinuston Formation (Lower Aalenian) in the vicinity of Bad Boll.

- (1) *Metacenoceras jurens*e (QUENSTEDT), Teufelsloch Member, *opalinum* Biohorizon, Heiningen clay pit, SMNS 70611/1 (leg. G. SCHWEIGEL).
- (2) *Hastites subclavatus* (VOLTZ), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/2 (leg. G. SCHWEIGERT).
- (3) *Acrocoelites conoideus* (OPPEL), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/3 (leg. R. MUNDLOS).
- (4) *Bositra buchi* (ROEMER), inset with close-up view of double-valved specimen, Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/4 (coll. E. KÖSTLIN).
- (5) *Toarctocera subpunctata* (MÜNSTER in GOLDFUSS), Teufelsloch Member, *dilucidum* Biohorizon, Pliensbach creek near Bad Boll, SMNS 70611/5.
- (6) *Ryderia doris* (ORBIGNY), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/6 (leg. G. SCHWEIGEL).
- (7) *Palaeonucula hammeri* (DEFRANCE), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/7 (leg. W. HAAG).
- (8) *Nicaniella voltzi* (GOLDFUSS), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/8 (coll. E. KOCH).
- (9) *Pseudomytiloides dubius* (SOWERBY), Teufelsloch Member, *dilucidum* Biohorizon, Heiningen clay pit, SMNS 70611/9 (leg. G. SCHWEIGERT).

Scale bar equals 50 mm.



Plate 28

Additional invertebrate fauna of the Opalinuston Formation (Lower Aalenian) in the vicinity of Bad Boll.

- (1) *Scaphotrigonia navis* (LAMARCK), Teufelsloch Member, Lucinenbank, Teufelsklingenbach creek, SMNS 70611/10.
 - (2) *Scaphotrigonia navis* (LAMARCK), in aragonitic preservation, Zillhausen Member, *hansrieberi* Biohorizon, Teufelsklingenbach creek, SMNS 70611/11 (leg. E. SCHNEIDER).
 - (3) *Pronoella trigonellaris* (SCHLOTHEIM), Zillhausen Member, Teufelsklingenbach creek, SMNS 70611/12 (coll. F. v. ALBERTI).
 - (4) *Mesomiltha plana* (ZIETEN), Zillhausen Member, *hansrieberi* Biohorizon, Teufelsklingenbach creek, SMNS 70611/13.
 - (5) *Scaphotrigonia navis* (LAMARCK), in calcitic preservation, Zillhausen Member, *hansrieberi* Biohorizon, Teufelsklingenbach creek, SMNS 70611/14.
 - (6) *Quenstedtia opalina* (QUENSTEDT), Teufelsloch Member, Teufelsklingenbach creek, SMNS 70611/15 (coll. E. KOCH).
- Scale bar equals 50 mm.

