



# Ammonites and stratigraphy of the Achdorf Formation (Braunjura Group; Aalenian) at the Wochenberg hill near Schömberg-Schörzingen (W Swabian Alb, SW Germany)

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# Abstract

In sections of the Achdorf Formation at the Wochenberg hill (western Swabian Alb, SW Germany), a succession of five ammonite biohorizons is distinguished (from bottom to top): the *crassicostatum* and *viallii* biohorizons of the Lower Aalenian (Bifidatum Subzone, Opalinum Zone) and the *latiumbilicus, discoidea*  $\alpha$  and *discoidea*  $\beta$  biohorizons of the Upper Aalenian (Murchisonae Subzone, Murchisonae Zone). The herein newly introduced *viallii* biohorizon is the youngest hitherto identified biohorizon of the Opalinum Zone (Bifidatum Subzone). A lectotype is designated for *Staufenia latiumbilicus* (Quenstedt, 1886), the index ammonite of the *latiumbilicus* biohorizon. The succession of biohorizons of the Murchisonae Subzone reflects the evolution of the graphoceratid late Aalenian ammonite genera *Staufenia* and *Ludwigia*.

# Keywords

Ammonite biohorizons, correlation, Germany, Graphoceratidae, Middle Jurassic, phylogeny

# 1. Introduction

The Upper Aalenian Achdorf Formation is an up to 60 metres thick series of claystones, arenaceous claystones and occasional limestone beds that crops out in the Wutach area as well as in the adjacent western and middle Swabian Alb (Franz and Nitsch 2009). Historically, this formation was lumped with a coeval succession of ferruginous sandstones of the Eisensandstein Formation in eastern Swabia and Franconia in the more biostratigraphically defined "Braunjura  $\beta$ ". The area of eastern Swabia had been well-known for its rich and diverse fossil content, namely ammonites, recovered from the long-abandoned iron mines in the vicinity of Aalen (Quenstedt 1856–1857; Oppel 1858) and was subsequently designated as name-bearing type area of the Aalenian Stage. In these

early days of stratigraphical investigations, only few Upper Aalenian ammonites from other areas in Swabia were reported. An exception is the area of the Wochenberg hill near Schömberg-Schörzingen. The Wochenberg is a hill located a few kilometres in front of the Upper Jurassic escarpment of the Swabian Alb. It is characterized by steep forested hillsides and an almost flat plateau formerly used for agriculture. Quenstedt (1886-1887) was the first to describe ammonites from there. Lörcher (1939) studied the litho- and biostratigraphy of several sections in the vicinity of Schörzingen and provided descriptions of the strata as well as their fossil content. The lithostratigraphic section and ammonites from this area were studied in greater detail by Rieber (1963) in his monograph on the ammonites of the "Braunjura \beta". Apart from ammonites, only few other groups of fossils were studied from the area of

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the Wochenberg hill. Recently, Weis in Weis et al. (2021) described a new species of the belemnite genus *Acrocoelites* based on specimens from the Untere Wilflingen-Bank (formerly: Comptum-Bank) of the Wochenberg hill.

Since natural outcrops along the steep hillsides of the Wochenberg only expose short intervals of the lithological succession, the complete section could only be roughly estimated in former times and the succession of ammonite faunas was still incompletely known. Moreover, extensive ammonite material housed in institutional and private collections mostly lacked detailed information about the exact locality and bed from where it was collected. These deficiencies hampered the recognition of evolutionary trends in ammonite lineages, sexual dimorphism, and changes of faunal composition through time as well as faunal migrations. Thus, the only possibility to add these missing data are excavations, where the complete succession is sampled bed-by-bed. This precise sampling of sections allows deciphering the ammonite evolution and results in a high-resolution biostratigraphy, although intraspecific variation within large samples complicates determinations.

The aim of this study, which focusses on the ammonites, is to present the scientific results of our excavations, which were executed between 2014 and 2022.

### 2. Material and methods

Our scientific excavations (2014-2018) of the Staufensis-Bank took place at the southwestern edge of the Wochenberg hill, southeast of a model airfield. Several hundred ammonites of the genera Staufenia and Ludwigia/Brasilia and a sole Planammatoceras were collected precisely bed-by-bed. Subsequently (2021-2022), the rock interval between the Untere Wilflingen-Bank and the Staufensis-Knollenlage was excavated at another section c. 20 metres further to the west of the previous one, with special focus on the ammonite-bearing Obere Wilflingen-Bank. In addition, two smaller excavations (2017, 2021) at a distance of c. 50 m and c. 170 m further southeast (in the direction to road L 435 connecting the town Schömberg and the village of Deilingen) focussed on the Untere Wilflingen-Bank. Additional sections of the Untere Wilflingen-Bank were sampled at the headwaters of the Schörzinger Starzel River and 350 m in southeastern direction, as well as along the steep escarpment of the Wochenberg hill north of road L 435.

The herein studied ammonites have been prepared mechanically using pneumatic chisels and airbrasive iron powder. All illustrated specimens are stored in the



Figure 1. Location map. The outcrops of the Middle Jurassic are marked in gray.

collection of the Staatliches Museum- für

collection of the Staatliches Museum- für Naturkunde in Stuttgart (acronym: SMNS). The specimens are illustrated in natural size, if not otherwise stated.

# 3. Description of the section

Our lithostratigraphic description of the uppermost Opalinuston and Achdorf formations starts from the bottom of the section. It is a combination of our recent observations and measurements and those of Rieber (1963). We studied in detail the interval from the Untere Wilflingen-Bank up to the Staufensis-Bank (sensu Rieber 1963).

### 3.1. Opalinuston Formation

Above the 'Wasserfallschichten' [Waterfall Beds] (c. 8.8 m; Rieber 1963, text-fig. 2) follows the 'sandige Tonmergel' [Sandy Clay-Marls] (8.6 m) with the 'Zopfplatten' [*Gyrochorte* Beds] (4–4.5 m); the latter are positioned in the upper half of the 'sandige Tonmergel' (Fig. 2).

## 3.2. Achdorf Formation

Untere Wilflingen-Bank [Lower Wilflingen Bed] (= uWB; c. 1.6 m; = Comptum-Bank sensu Rieber 1963)

**Figure 2.** Section at the southern slope of the Wochenberg hill (modified after Rieber 1963, fig. 2 [Profil c]; the beds below the Wilflingen-Bank were not studied). The Obere Wilflingen-Bank is separately shown in Fig. 4. (W. F. = Wedelsandstein Formation, Sow.-Ool. = Sowerbyi-Oolith, Staufensis-B. und St.-B. = Staufensis-Bank, ?Sinon-B. = ?Sinon-Bank, Ob. Wilflingen-B. und oWB = Obere Wilflingen-Bank, Unt. Wilflingen B. und uWB = Untere Wilflingen-Bank, Subz. = Subzone, Murch. = Murchisonae, Co.= Concavum, St-B = Staufensis-Bank).



The Untere Wilflingen-Bank (formerly: Comptum-Bank, see Dietze et al. 2021a) consists of a chamosite-oolitic, gray-green to dark brown marly limestone, partly rich in fossils. In our excavation sites at the southern hillside of the Wochenberg, most ammonites occurred in the well-lithified beds uWB-4 and uWB-7. The thicknesses and lithologies of individual beds are almost identical in both sections. In other outcrops at the headwaters of the Schörzinger Starzel River, the Untere Wilflingen-Bank has an overall similar thickness, but at each section it shows some variation in respect of the thickness and lithology of individual beds. Like in our two excavation sites at the Wochenberg hill, the ammonites occur in two layers located in more or less the same position within the Untere Wilflingen-Bank. The frequency of ammonites in both fossiliferous horizons varies at the various localities.

- Bed uWB-1 (0.15 m): arenaceous clayey marls with weathered lithified limestone portions, yellow to beige.
- Bed uWB-2 (0.15 m): arenaceous marly limestone, occasionally with lithified portions of strongly weathered marly limestone, rusty.
- Bed uWB-3 (0.15 m): clayey marl, gray in its upper part; with a yellow-beige layer in its middle.
- Bed uWB-4 (0.4–0.5 m): lithified calcareous marl, partly chamosite-oolitic, partly arenaceous, with abundant ammonites and bivalves.

Bivalves: Isocardia cordata Buckman, Gresslya sp., Clavitrigonia brodiei (Lycett), Cl. sp. (small-sized), Pholadomya fidicula Sowerby, Entolium demissum (Phillips), Astarte elegans Sowerby, Inoperna sowerbyana (d'Orbigny), Parvamussium pumilus (Lamarck). Ammonites are concentrated slightly above the middle of the bed. Occasionally with a poorly lithified marly limestone layer (0.05 m) located slightly below the middle of the bed. In the latter case, the ammonites occur in the lower part of the bed.

Ammonites: Leioceras crassicostatum [M], L. goetzendorfense [M], L. paucicostatum [m], L. striatum [m]

- Bed uWB-5 (0.1–0.2 m): lithified calcareous marl, more marly developed at its base.
- Bed uWB-6 (0.08–0.1 m): unconsolidated, rusty calcareous marl.
- Bed uWB-7 (0.4–0.5 m): chamosite-oolitic or arenaceous, very hard bluish-gray calcareous marl, which splits into three separate beds when weathered. The bluish-gray calcareous marls exhibit a brown-beige weathering rim. Fossils are extremely rare. Above the basal layer (c. 0.1 m) follows a thin rusty layer. Usually, the only ammonites occur c. 0.15–0.2 m below the top of the bed within a 0.01 to 0.1 m thick layer of shell debris separating the two upper partial beds. Ammonites: *L. goetzendorfense* [M], *L. paucicostatum* [m], *L. striatum* [m]
- Bed uWB-8 (0.1 m): lithified calcareous marl.
- Bed uWB-9 (0.3 m) arenaceous clayey marl.

Ammonites: *L. goetzendorfense* [M]

- Bed uWB-10 (0.1 m): nodular calcareous marl.
- Tonmergel [Clay-Marl] (c. 3.2-4 m): this unit was not exposed and could not be studied. At the southern hillside of the Wochenberg we measured a vertical distance of c. 12-13 m between the top of the Untere Wilflingen-Bank (= Comptum-Bank sensu Rieber 1963) and the top of the Staufensis-Bank. This is in contrast to Rieber (1963, text-fig. 2, Profil c), who reported a much greater thickness of c. 24 m for this interval. After our new measurements, the vertical distance between the basis of the Obere Wilflingen-Bank [Upper Wilflingen Bed] and the top of the Untere Wilflingen-Bank [Lower Wilflingen Bed] is only 3.2-4 m (variable in different sites along the southern escarpment) and not 17.5 m as mentioned by Rieber (1963, text-fig. 2, Profil c Wochenberg). Rieber (1963) interpolated the distance between the "Comptum"-Bank up to the Staufensis-Bank across the Wochenberg hill from the northern to the southern hillside in several steps; this procedure may have resulted in significant measurement errors.



**Figure 3.** Section of the Obere Wilflingen-Bank at the southern slope of the Wochenberg hill (*viallii* biohorizon, Bifidatum Subzone, Opalinum Zone, Lower Aalenian).

#### Obere Wilflingen-Bank [Upper Wilflingen Bed] (1.6-

1.7 m; Fig. 3)

In one of his sections, Rieber (1963, text-fig. 2, Profil c) showed a separate bed with a maximum thickness of 1 m that follows at a vertical distance of 14 m above the Untere Wilflingen-Bank. It seems that this obviously discontinuously developed bed may reach even greater thicknesses at some places of the Wochenberg hill. In the Katzensteige section near Gosheim, Rieber (1963 text-fig. 2, Profil b) termed a c. 1.45 m thick bed following 3.3 m above the "classical" ammonite-bearing "Comptum"-Bank **["Comptum"-Bed]** (= Untere Wilflingen-Bank) as well as "Comptum"-Bank. This is why we refer to the higher bed as 'Obere Wilflingen-Bank'.

- Bed oWB-1 (0.3 m): the 0.2 m thick lower part of this bed (oWB-1a) consists of brown arenaceous calcareous marl with bluish-gray hard limestone lenses. The upper 0.1 m thick portion of the bed (oWB-1b) consists of a brown to brick-red marly limestone with abundant compressed ammonites. Ammonites (bed oWB-1b): Ancolioceras sp. [M], Leioceras sp. [M]
- Bed oWB-2 (0.25 m): same lithology as bed oWB-1a; from a calcareous lense within this bed, a single specimen of Ancolioceras subfalcatum was recovered. Ammonite: Ancolioceras subfalcatum [M]
- Bed oWB-3 (0.3 m): marly limestone, gray, brown in weathered state, with layers of compressed ammonites.

Ammonites: Ancolioceras sp. [M], Leioceras sp. [M]

- Bed oWB-4 (0.05 m): clayey marl, gray.
- Bed oWB-5 (0.05–0.1 m): lithified marly limestone, brown.

Ammonites: Leioceras sp. [?M]

 Bed oWB-6 (0.2-0.25 m): marly limestone, weakly lithified, brown, with small limestone nodules (diameters 0.01-0.02 m). In its upper part layers with mostly compressed ammonites.
 Ammonites: Leioceras evertens [M], L. goetzendor-

fense [M], Ancolioceras subfalcatum [?m] Bed oWB-7 (0.1–0.13 m): marly limestone, weak-

Is bed own-7 (0.1-0.13 m). Thany inflectore, weakly lithified, with lenses of gray, hard limestone with a brownish weathering rim. Most of the limestone lenses did not contain fossils; a few of them contained shell fragments, and only a single one yielded a couple of ammonites.

Ammonites: Ancolioceras noszkyi [M], A. viallii [M]

 Bed oWB-8 (0.1-0.15 m): clayey marl, gray in unweathered state; compressed ammonites occur frequently in layers.

Ammonites: Leioceras goetzendorfense [M], Ancolioceras sp. [M]

Bed oWb-9 (0.1–0.2 m): the lithology of this bed changes significantly within distances of a few metres. At the left side of our excavation at the southern hillside of the Wochenberg it is developed as a brown calcareous marl (0.1–0.13 m), partly rusty, containing hard, splintery gray limestone nodules almost lacking fossils, only occasionally with shell debris (up to 0.3 m in diameter), with a rusty-brown weathering rim. In the opposite side of our excavation, this bed is thicker (0.2 m) and there, the upper c. 0.05 m of the bed, which is developed as a densely packed bivalve shell bed, are commonly split off. The lower part of the bed (c. 0.15 m) is a gray-bluish

limestone. Most ammonites occur in the marginal part of the nodules or of the limestone bed and reach at least partly the rusty oxidation zone; only few ammonites occurred in the centre of the limestone nodules or in the centre of the bed. Apart from a few marly layers with a relatively rich ammonite content, the majority of ammonites from the Obere Wilflingen-Bank originates from bed 9. In all other parts of the Obere Wilflingen-Bank ammonites are extremely rare. Only bed oWB-9 could be intensively sampled.

Ammonites: Ancolioceras aff. subacutum [M], A. citaae [M], A. viallii [M], A. cf. viallii [M], A. krymholzi [M], A. subfalcatum [M], A. aff. substriatum [m], Leioceras goetzendorfense [M], L. capillare [M], L. striatum [m].

Marly limestone (1.9 m): brown, c. 0.2–0.3 m above its basis with a layer of small gray limestone nodules (c. 0.05–0.1 m in diameter) surrounded by layered rusty weathering rims; numerous burrows. Ammonites: Ancolioceras sp.

- Limestone / marly limestone (c. 0.8 m; = ? Sinon-Bank sensu Rieber 1963, text-fig. 2, Profil c): At the very steep southern hillside of the Wochenberg which is thickly covered with soil and talus, this interval could only be localized at two small places. We did not find any ammonites there, but an intensive sampling of this bed was hampered by the steep slope. It is possible that a small sample of well-preserved ammonites from the Wochenberg hill in the G. and U. Bayer collection (SMNS) originates from this interval; however, the exact position of these ammonites (which are preserved in a shelly matrix) within the section, is unknown.
  - (0.05–0.1 m): hard, splintery, laterally thinning lenses of gray limestone with pyrite, no macrofossils recorded.
  - (0.0-0.2 m): weakly lithified marly limestone, brown.
  - (0.6 m): alternation of limestone, calcareous marl and marly limestone.
    - 0.1–0.2 m: limestone, mainly consisting of fine bivalve shell debris.
    - 0.02–0.04 m: weakly lithified marly limestone, brown, partly pinching out.
    - 0.1–0.12 m: splintery limestone, gray, no macrofossils recorded.
    - 0.25–0.3 m: several gray, irregularly thinning platy limestone benches with small lithoclasts, separated by lithified brown marly limestone. Between the limestone benches *Zoophycos* burrows occur. A massive bed in fresh state.

**Clayey marl** (c. 1.1–1.3 m): clayey to marly limestone, brown (not studied in detail).

Arenaceous limestone (0.9 m) [= Sehndensis-Knollenlage sensu Rieber 1963, text-fig. 2, Profil c): at our excavation site, this interval was developed as uniform bed. In fresh state, the bluish to brown bed is splintery hard and apparently lacking macrofossils. In weathered state, it splits into several smaller beds. No ammonites were found.

Ammonites: *Staufenia "sehndensis"* [after Rieber 1963; SMNS, ex coll. G. and U. Bayer]

- **Clayey marl** (0.8–0.9 m): arenaceous, thin-bedded, brown-yellow, with rare reworked limestone pebbles, ichnofossils (*Zoophycos*) and occasional bivalves (*Pholadomya* sp.). The lowermost 0.1 m are lithified and amalgamated with the underlying calcareous marl.
- Staufensis-Bank (sensu Rieber 1963; 1.2-1.6 m): The thicknesses of individual beds within the Staufensis-Bank varies significantly over short distances. However, this variation does not hamper the recognition and correlation of these beds. Contrary to Rieber (1963), our new observations revealed that the uppermost layers are completely eroded at the Wochenberg hill. Since the lithostratigraphic term 'Staufensis-Bank' is defined in the wider area as the uppermost thicker set of limestones following below the Concava-Bank, we used the term Staufensis-Bank despite of this erosional lack of its uppermost part which otherwise yields the name giving index fossil Staufenia staufensis. The shell beds mainly contain small-sized ammonites, occasionally also larger-sized ones. Most specimens occur on the surfaces of several smaller beds into which the Staufensis-Bank can be split.
  - Bed St-B 1 (0.1–0.2 m): soft, marly limestone, brown-yellowish, rusty, lacking macrofossils.
  - Bed St-B 2 (0.05–0.1 m): soft, either an arenaceous marly limestone, or developed as a hard limestone with a bluish core; the only recorded macrofossil is the ichnofossil *Zoophycos*. Together, beds St-1 and St-2 have a constant thickness of 0.2 m.
  - Bed St-B 3 (0.05-0.1 m): marly limestone with poorly preserved, compressed *Staufenia* sp. Complete phragmocones are often locally accumulated, but nearly absent at other places.
  - Ammonites: *Staufenia latiumbilicus* [M] **Bed St-B 4** (0.1–0.15 m): flaser-bedded calcareous
  - and of bluish colour, marginally brown; poorly fossiliferous, rare accumulations of nuclei of Staufenia, bivalves and shell debris. Ammonites: St. latiumbilicus [M]
  - Bed St-B 5 (0.25–0.35 m): irregularly flaser-bedded arenite layers separated by platy shell beds with abundant bivalves (*Mytiloceramus* sp., *Meleagrinella*
  - *elegans* (Munier-Chalmas)) and ammonites (almost exclusively *St. latiumbilicus*, only very rare fragments of *Ludwigia*), partly chamosite-oolitic.

Ammonites: St. latiumbilicus [M and m], Ludwigia aff. crassa [M], L. armipotens [M], L. cf. subtuberculata [m]

 Bed St-B 6 (0.05–0.15 m): arenaceous marly limestone, occasionally weathered with a rusty rim and a soft, ochre-coloured core. With lenses of bivalve shell debris containing small ammonites (almost exclusively *Staufenia*).

Ammonites: St. discoidea  $\alpha$  [M and m], Ludwigia tuberata [M], Brasilia howarthi [M]

- Bed St-B 7 (0.05–0.15 m): soft marly limestone with burrows, compressed *Pholadomya* sp., belemnites, very rare ammonites (three specimens).
   Ammonites: *St. discoidea* α [M], *Ludwigia murchi*sonae [M], *L. subtuberculata* [m]
- Bed St-B 8 (0.4–0.6 m): compact, partly arenaceous marly limestone divisible into three subunits:
  - Bed St-B 8a (0.1 m): irregularly flaser-bedded arenaceous marly limestones; with platy or rusty layers at the very base. *Ludwigia* spp. locally very abundant, with large-sized specimens over 20 cm in diameter, accompanied by nuclei and phragmocones of *Staufenia*, rarely with complete bodychamber.

Ammonites: St. discoidea α [M and m], Ludwigia depilata [M], L. cf. depilata [M], L. tuberata [M], L. armipotens [M], L. reflua [M], L. murchisonae [M], L. subtuberculata [m], Brasilia theobaldi [M], B. elmii [M], B. falcatiformis [M]

 Bed St-B 8b (0.1-0.25 m): arenaceous marly limestone, intercalated with layers of shell debris; bivalves (*Mytiloceramus* sp., *Meleagrinella elegans* (Munier-Chalmas)) and ammonites are abundant. *Staufenia* is common, partly preserved with bodychamber; *Ludwigia* spp. are rarer than in bed St-B 8a.

Ammonites: St. discoidea α [M and m], Ludwigia depilata [M], L. tuberata [M], L. murchisonae [M], L. armipotens [M], L. reflua [M], L. subtuberculata [m], Brasilia baldii [M], B. theobaldi [M], B. falcatiformis [M], B. howarthi [M]

Bed St-B 8c (0.15-0.25 m): occasionally, the top of the Staufensis-Bank is formed by an up to c. 8 cm thick marly limestone; sometimes this bed is platy or arenaceous. In most other cases, it was formed by a 2-3 cm thick bed. Most ammonites were recovered from a discontinuous bivalve shell bed that occurred in the uppermost 10-15 cm of the Staufensis-Bank.

Ammonites: St. discoidea β [M and m], Ludwigia aff. murchisonae [M], L. fueloepi [M], L depilata [M], L. reflua [M], L. gradata [M], Brasilia bradfordensis [M], B. elmii [M], Planammatoceras aff. planinsigne [M]

Clayey marl (0.05-0.1 m).

**Clayey marl** (0.1 m): with scattered siderite concretions, often rusty weathered.

**Quaternary cover** (0.3–0.8 m): up to the surface c. 0.3–0.8 m talus, loam and soil.

The beds of the **Concava-Bank** and the **Sowerbyi-Oolith** (Rieber 1963) should be expected in a distance of c. 2 m above the top of the Staufensis-Bank; however, these beds were not present at our excavation sites. We were even unable to locate these beds anywhere else at the Wochenberg hill, except of its northern hillside, beyond the road L 435.

### 4. Description of the ammonite faunas

#### 4.1. Preliminary remarks

Within Graphoceratidae, the Staufenia lineage is easily divisable into a succession of only moderately variable chronospecies. In contrast, the taxonomy of Leioceras/ Ancolioceras and Ludwigia/Brasilia is much more complex. There are no focussed evolutionary trends observable, and some morphologies can reappear independently multiple times. Moreover, ammonites of these groups vary considerably within a single biohorizon. Plenty of the recorded morphologies are not restricted to a single biohorizon, but range within several succeeding ones. Finally, from some well-sampled Aalenian beds such as the Scissum Bed of southern England (Buckman 1887-1907) or the Lower/Upper Aalenian transition of Bakonycsernye in Hungary (Géczy 1967) an extremely large number of potentially valid taxa were formally described. However, few or no nominal taxa of this time interval were reported from other regions. The distinction of these nominal taxa is difficult. Considering the great variation within this group of ammonites, both in coeval beds as well as in a succession of beds, it is disputable whether to assign a specimen to a taxon described from a stratigraphically older or younger bed. Adding new taxa would even complicate this taxonomic maze. Therefore, both in Leioceras/Ancolioceras and Ludwigia/Brasilia new species should be only introduced based on very strong arguments in favour. Fortunately, this was not necessary in the course of this study.

Despite the partly large samples recovered by bed-by-bed sampling it was often impossible to identify corresponding macroconchs (M) and microconchs (m) – females and males – with accuracy. Specimens of the Tethyan genera *Planammatoceras* and *Tmetoceras* are very rare.

# 4.2. The ammonite fauna of the Untere Wilflingen-Bank [= Comptum-Bank auct.]

The ammonite fauna of the Untere Wilflingen-Bank (formerly: "Comptum-Bank") in the western Swabian Alb was described by Rieber (1963) in great detail. He determined coarsely ribbed and broad macroconchiate specimens as *L. crassicostatum* Rieber; all other macroconchs were assigned to *L. comptum* (Reinecke). In the microconchs, the coarser ribbed forms were distinguished as *L. paucicostatum* Rieber (the holotype of the latter species originates from the Wochenberg hill), and the weakly sculptured ones as *L. striatum* (Buckman). Concerning the microconchs, we follow the classification and determinations by Rieber (1963). For the sake of completeness, we

here illustrate one example of L. striatum (Fig. 4.5) and one of L. paucicostatum (Fig. 4.9). It is remarkable that at the Wochenberg hill and in the headwaters of the Schörzinger Starzel River microconchs are significanthy more common than in the sections at Gosheim located only a few kilometres farther to the southwest. A possible reason for this variation might be that both living and preservational conditions for microconchs had been more favorable in the present day Wochenberg area due to a calmer environment (Rieber 1963). In Gosheim, macroconchiate specimens of Leioceras with a better rounded bodychamber are more common than at the Wochenberg hill. Thus, we cannot exclude a slight difference in age of the Untere Wilflingenbank at both places; however, this difference is below the biostratigraphical resolution. The former determination of the macroconchs as 'L. comptum' must be rejected since the rediscovered holotype of Reinecke's Nautilus comptus was found to be a latest Toarcian Pleydellia (Chandler and Callomon 2010). The Leioceras specimens illustrated in Fig. 4 provide an overview on the great variation within adult macroconchs from the Wilflingen-Bank at the Wochenberg hill. We assigned them to the two morphospecies L. crassicostatum Rieber (Fig. 4.1a, b) and – following Chandler and Callomon (2010) – L. goetzendorfense (Dorn) (Fig. 4.2a-4b, 8a, b, 10a, b). Extreme morphologies are very rare (Fig. 4.1a, b [broad section, extremely coarse-ribbed  $\rightarrow$  transitional to Ludwiga]; Fig. 4.10a, b [high section  $\rightarrow$  transitional to Ancolioceras]). In contrast to the illustrated material, most macroconchiate graphoceratids from the Wilflingen-Bank are juveniles. They still lack the typical rounded venter, which is only well developed on the bodychamber of adults. However, the bulk of our specimens is close to the morphology of the specimen illustrated in Fig. 4.4 (compare the specimens in Rieber 1963, pl. 1, figs 2-4, 8, 9, 12, 14).

*Tmetoceras scissum* (Figs 4.6a, b, 7a, b; Rieber 1963) is a rare Tethyan immigrant in the Jurassic of Swabia (Dietze and Schweigert 2020). Unfortunately, a perfectly preserved specimen of c. 45 mm diameter was lost during preparation.

# 4.3. The ammonite fauna of the Obere Wilflingen-Bank

The taxonomy and determination of the ammonites from the Obere Wilflingen-Bank is extremely complicated, since the stratigraphical position of this fauna is transitional between formally named taxa from older horizons of the Bifidatum Subzone (Opalinum Zone) and younger ones of the Haugi Subzone (Murchisonae Zone), similarly to the recently described case of the slightly younger *subfalcatum* biohorizon (Dietze et al. 2021b). Usually, the ammonites of the (Untere) Wilflingen-Bank both, in the eastern and western Swabian Alb, are classified in a few macroconchiate and microconchiate taxa (*L. "comptum"*, *L. evolutum*, *L. crassicostatum* and *L. striatum*, and *L. paucicostatum*, respectively) (Rieber 1963; Dietze et al. 2021a). By contrast,



Figure 4. (1a, b) Leioceras crassicostatum (Rieber) [M], SMNS 70640/1. (2a–4b, 8a, b, 10a, b) L. goetzendorfense (Dorn) [M]; (2) uWB-4, SMNS 70640/2; (3) uWB-7, SMNS 70640/3. (4) uWB-4, SMNS 70640/4; (8) uWB-8, SMNS 70640/5; (10) SMNS 70640/6. (5) L. striatum (Buckman) [m], SMNS 70640/7. (6a–7b) Tmetoceras scissum (Benecke); (6) SMNS 70640/8; (7) uWB-4, SMNS 70640/9. (9) L. paucicostatum Rieber [m], SMNS 70640/10. 2–4, 6, 8: southern slope of the Wochenberg hill. 1, 5, 7, 9, 10: headwaters of the Schörzinger Starzel river. 1–10: Achdorf Formation, Untere Wilflingen-Bank, Lower Aalenian, Opalinum Zone (Bifidatum Subzone), crassicostatum biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



Figure 5. (1, 11, 13) *Ancolioceras subfalcatum* (Buckman) [M and ?m]; (1) oWB-2, SMNS 70640/74; (11) oWB-9, SMNS 70640/90; (13) oWB-6, SMNS 70640/75. (2) *Leioceras* sp. [?M], oWB-5, SMNS 70640/76. (3) *A. viallii* (Géczy) [M], oWB-7, SMNS 70640/81. (4) *L. evertens* (Buckman) [M], oWB-6, SMNS 70640/77. (5) *A. noszkyi* (Géczy) [M], oWB-7, SMNS 70640/80. (6) *A. krymholzi* (Géczy) [M], oWB-9, SMNS 70640/84. (7) *A.* sp. [M], oWB-9, SMNS 70640/85. (8) *L. goetzendorfense* (Dorn) [M], oWB-6, SMNS 70640/78. (9, 16) *L. striatum* (Buckman) [M]; (9) oWB-7, SMNS 70640/82; (16) oWB-9, SMNS 70640/83. (10, 15) *L. capillare* (Buckman) [M]; (10) oWB-9, SMNS 70640/83. (12) oWB-9, SMNS 70640/93. (12, 14) *A.* aff. *substriatum* (Buckman) [m]; (12) oWB-9, SMNS 70640/93. (14) oWB-9, SMNS 70640/91. 1–16: Obere Wilflingen-Bank, southern slope of the Wochenberg hill; Opalinum Zone (Bifidatum Subzone), *viallii* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



Figure 6. (1) Ancolioceras citaae (Géczy) [M], oWB-9, SMNS 70640/87. (2) A. cf. viallii (Géczy) [M], oWB-9, SMNS 70640/97. (3) A. aff. subacutum (Buckman) [M], oWB-9, SMNS 70640/92. (4, 5) A. viallii [M]; (4) oWB-9, SMNS 70640/88; (5) oWB-9, SMNS 70640/89. (6): Leioceras goetzendorfense (Dorn) [M], oWB-8, SMNS 70640/79. 1–6: Obere Wilflingen-Bank, southern slope of the Wochenberg hill; Opalinum Zone (Bifidatum Subzone), viallii biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

in Ancolioceras from the Haugi Subzone of the Wutach area and the eastern Swabian Alb plenty of nominal species and varieties are distinguished (Horn 1909; Dietze et al. 2021b). There is a gradual transition between the (morpho-)genera Leioceras and Ancolioceras (see Dietze et al. 2021b). The ammonites from the Obere Wilflingen-Bank exhibit numerous combinations of characters of nominal species, which hampers the determination of individual specimens. We classified all graphoceratid ammonites from the Obere Wilflingen-Bank either as Leioceras Hyatt, 1867 or Ancolioceras Buckman, 1899 [in Buckman 1887-1907] and considered further taxa mostly introduced by Buckman (1887–1907) (e.g., Cypholioceras, Cylicoceras, Geyerina, Hyattina, Mansellia, etc.) as subjective younger synonyms. Their continuous usage would make ammonite taxonomy from the Lower/Upper Aalenian transitional beds extremely complicated.

A relatively small ammonite with a ventrally rounded bodychamber bearing a prominent ribbing (Fig. 5.4) is determined as *Leioceras evertens* (Buckman, 1899 [in Buckman 1887–1907]). Several ammonites with a rounded bodychamber are assigned to *Leioceras goetzendorfense* (Dorn, 1935) (Figs 5.8, 6.6); they are morphologically indistinguishable from ammonites of the Untere Wilflingen-Bank of the western Swabian Alb. Two relatively involute *L. capillare* (Buckman, 1928 [in Buckman 1909–1930]) are poorly sculptured and exhibit only a weakly developed ventral shoulder (Figs 5.10, 5.15). Similarly, two microconchiate *L. striatum* (Buckman, 1899 [in Buckman 1887– 1907]; Figs 5.9, 5.16) are mophologically almost identical with specimens of the Untere Wilflingen-Bank.

Due to the gradation from the genus Leioceras into the genus Ancolioceras, some specimens cannot be assigned with confidence to the one or the other genus. Specimens closely resembling L. goetzendorfense (compare Rieber 1963, pl. 1, fig. 12), but with a more regular ribbing than developed in most graphoceratids from the Untere Wilflingen-Bank and showing a fastigate venter until the aperture (Figs 5.3; 6.4, 6.5), are included in Ancolioceras viallii (Géczy, 1967). One specimen exhibits the typical ribbing style of A. viallii, but has a very broad section with a rounded venter on the bodychamber (Fig. 6.2); it is clearly intermediate between the genera Leioceras and Ancolioceras and here determined as A. cf. viallii (Géczy). A. noszkyi (Géczy, 1967) (Fig. 5.5) has a very fine ribbing. Specimens determined as A. krymholzi (Géczy, 1967) (Fig. 5.6) and A. subfalcatum (Buckman, 1899 [in Buckman 1887–1907]) (Figs 5.1, 5.11; 5.13) are close to the majority of ammonites of the subfalcatum biohorizon (Dietze et al. 2021b). A. citaae (Géczy, 1967; Fig. 6.1) is recorded from the subfalcatum biohorizon as well. There is a striking resemblance of the latter with the holotype of Cylicoceras undatum Buckman, 1899 [in Buckman 1887-1907]; however, the latter originates from much older beds (opaliniformis hemera) at Haresfield Hill in South England. A. citaae differs from L. crassicostatum Rieber, 1963 by its more slender whorl section, a more involute umbilicus and a slightly higher whorl section. These three species (C. undatum, A. citaae and L. crassicostatum) represent morphological extremes within the intraspecific variation of the respective chronospecies (Dietze et al. 2021a). In lateral view, Ludwigia praecursor Rieber, 1963 looks very close to A. citaae, however, it is distinguished by its ventrally forwardly bended ribs. A very involute, high-sectioned and large-sized specimen (Fig. 6.3) with a sharp venter and a uniform ribbing style is close to A. subacutum (Buckman, 1899 [in Buckman 1887–1907]). Our specimen differs from the latter by a higher number of intercalatory ribs; hence, we prefer a determination in open nomenclature as A. aff. subacutum. A. costatum (Buckman, 1888 [in Buckman 1887–1907]) is another similar form which exhibits characteristic shovel-like thickenings of the ribs on the bodychamber. Two microconchiate specimens (Figs 5.12, 5.14) are assigned to A. aff. substriatum (see Dietze et al. 2021b, pl. 5, fig. a1, 2), since A. subfalcatum is based on a macroconch.

# 4.4. The ammonite faunas of the Staufensis-Bank

#### 4.4.1. latiumbilicus biohorizon

#### Genus Staufenia Pompeckj, 1906

Graphoceratids of the genus Staufenia from beds St-B 3-5 (latiumbilicus biohorizon) are generally assigned to Staufenia latiumbilicus (Quenstedt, 1886). Quenstedt (1886, pl. 57, Figs 8, 14) figured two specimens from the Wochenberg hill as Ammonites discus latiumbilicus that are illustrated herein (Figs 10.1a, b and Fig. 9.6a, b). Quenstedt (1886, p. 462, 464) mentioned that the species name refers to the relatively wide umbilicus of this ammonite. Since Quenstedt's third names are considered as subspecies (ICZN 2005) and the taxon latiumbilicus is neither preoccupied (Hölder 1958) nor a nomen oblitum (see e.g. Hoffmann 1913: 113; Rieber 1963: 42; Contini 1969: 32), the specific name St. latiumbilicus must be considered as valid (ICZN 1999, Art. 46). For the taxonomic stability, we here designate one of Quenstedt's syntypes (1886, pl. 57, fig. 8) as the lectotype (Fig. 10.1a, b).

For an exhaustive description of St. latiumbilicus we refer to Rieber's (1963) description of St. sehndensis, since he described St. latiumbilicus under that name. The previous identification of specimens from the latiumbilicus biohorizon as St. sehndensis (Hoffmann) should be abandoned after the formal validation of Quenstedt's third names. The taxon St. sehndensis, originally described from North Germany, is either a younger subjective synonym of St. latiumbilicus or a morphologically very close predecessor of St. latiumbilicus. Since the latiumbilicus biohorizon at the Wochenberg hill is the type horizon and locality of St. latiumbilicus, the herein documented specimens are topotypes. Hoffmann (1913: 114), when introducing St. sehndensis, mentioned that only the fact that Quenstedt (1886, pl. 58, fig. 5) misidentified one of his specimens as Ammonites discoideus prevented him to use "Ludwigia" latiumbilica (Qu.) instead of introducing a new species, "Ludwigia" sehndensis. At his time, designation of a lectotype, which would have avoided any confusion, was not common practice. Hoffmann (1913: 116) clearly mentioned a medium-sized specimen (pl. 6, fig. 4, text-fig. 1) (Fig. 9.4a, b) being the type of his new species *"Ludwigia" sehndensis*, what we must take as a holotype designation. Consequently, the longstanding opinion (Rieber 1963; Schlegelmilch 1985) that the loosely collected specimen of Hoffmann (1913, pl. 4, fig. 3) was the lectotype is erroneous. Both, Hoffmann (1913: 3) and Rieber (1963) interpreted *Staufenia sehndensis* as a chronospecies with which we concur.

The maximum size of Staufenia latiumbilicus is represented by a specimen of nearly 30 cm diameter (Fig. 8.5a, b). The unusually large size and the rounded umbilical edge of this specimen not developed in any other representatives of this species points to a pathology. Specimens with preserved bodychamber (Fig. 7.1a, b) are very rare; most specimens are phragmocones with a rather uniform diameter of c. 16-17 cm (Fig. 10.2a, b). Inner whorls can be smooth (Fig. 7.5), weakly ribbed (Fig. 7.4) or coarser ribbed (Fig. 9.1, 3). The ammonite illustrated in Fig. 9.3 and the holotype of St. sehndensis (Fig. 9.4a, b) are almost identical. The specimen of Staufenia Fig. 9.7 is strikingly similar to the paralectotype of St. latiumbilicus (Fig. 9.6a, b), except for the slightly earlier beginning of the egression of the bodychamber as indicated by the preserved spur line. The specimen of Fig. 9.5 is still reminiscent to Ancolioceras.

Microconchiate *St. latiumbilicus* vary in a wide range from almost smooth (Fig. 8.4), weakly ribbed (Fig. 7.3) to coarsely ribbed specimens (Fig. 7.2; Fig. 8.3a, b).

#### Genus Ludwigia Bayle, 1878

In the latiumbilicus biohorizon of the Wochenberg hill, ammonites of the genus Ludwigia are extremely rare. Besides c. 65 specimens of Staufenia only three fragmentary Ludwigia were recorded from bed St-B 5. These are morphologically intermediate between Ludwigia specimens from the opalinoides biohorizon below and those from the discoidea a biohorizon above; the ribbing is not falcate but only falcoid, like in most early representatives of the opalinoides biohorizon of the western Swabian Alb. In contrast to these early representatives, the younger forms of the latiumbilicus biohorizon lack the ventral bending of the ribs towards the aperture (Horn 1909, pl. 12, figs 1-7, pl. 13, figs 1-2; Rieber 1963, pl. 4, figs 3-9). Instead, the keel is laterally bordered by an unsculptured band, like in the younger "Artengruppe der L. murchisonae" (Rieber 1963, pl. 5, figs 7, 8, 14-17; Ureta Gil 1983, pl. 9, fig. 7). In our determinations, we focussed on the falcoid ribbing style of the stratigraphically older Ludwigia taxa and assigned the specimens from the latiumbilicus biohorizon to L. aff. crassa (Horn, 1909) (Fig. 8.1a, b) and L. armipotens (Buckman, 1904 [in Buckman 1887–1907]) (Fig. 8.2a, b), respectively.

#### Genus Planammatoceras Buckman, 1922 [in Buckman 1909–1930]

Rieber (1963, pl. 8, fig. 10) illustrated an excellently preserved *Planammatoceras planiforme* (Buckman, 1922 [in Buckman 1909–1930]) from the *latiumbilicus* biohorizon of the Wochenberg hill.

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#### 4.4.2. *discoidea* α biohorizon

#### Genus Staufenia Pompeckj, 1906

The ammonites of the genus Staufenia from the interval St-B 6 to St-B 8b represent Staufenia discoidea (Quenstedt, 1886). Hoffmann (1913) designated the specimen from Schörzingen (= W or S hillside of the Wochenberg) illustrated by Quenstedt (1886, pl. 58, fig. 3) (Fig. 11.6a, b) as lectotype of St. discoidea. Accoring to its morphology, it originates from the discoidea a biohorizon. For an exhaustive description of St. discoidea we refer to Rieber (1963: 44). At the Wochenberg hill, the succession of an older St. discoidea a and a younger St. discoidea  $\beta$  form can be recognized (Fig. 21). In St. discoidea a, the umbilicus in juvenile and median stages is wider and the spur line of the outer whorl egregates less rapidly than in St. discoidea  $\beta$  (e.g., St. discoidea  $\alpha$  in Figs 11.1a, b, 5 and St. discoidea β in Figs 18.1, 18.4, Fig. 21, respectively). In complete adults (Fig. 13.1), the egregation of the bodychamber exceeds the mid-flank of the previous whorl. The maximum adult size of St. discoidea a reaches 25 cm, but most specimens are much smaller. The conchs become smooth at diameters of at least 50-60 mm so that larger specimens are remarkably similar to one another, except for the presence and strength of primary ribs in the umbilicus (Figs 11.1a, b, 11.5, 13.1, 14.3a, b). The sculpture of inner whorls can be almost smooth as in the lectotype of St. discoidea (cf. Figs 11.6a, b, 12.1, 13.3), weakly ribbed (Fig. 12.2; Fig. 13.4) or even coarse-ribbed (Fig. 12.3a, b). Some of the smooth-shelled inner whorls are still reminescent to the ancestral genus Ancolioceras. Microconchs, here termed as St. discoidea a [m], are either involute and weakly ribbed (Figs 11.2a, b, 13.2, 5), slightly stronger ribbed (Fig. 11.3a, b) or coarse-ribbed and evolute (Figs 11.4a, b, 13.6). Among macroconchs, specimens with weakly sculptured inner whorls predominate, whereas among the microconchs the coarse-ribbed evolute forms are more common. The sculpture continues up to the aperture in the microconchs; sometimes it weakens a little. When preserved, the microconchs show a spatulate apophysis (Fig. 13.5).

St. latiumbilicus is more evolute than St. discoidea  $\alpha$  and exhibits a more gradational egregation of the outer whorl as indicated by the preserved spur line (Fig. 21).

#### Genera Ludwigia Bayle, 1878 and Brasilia Buckman, 1899 [in Buckman 1887–1907]

Concerning macroconchs, in the *discoidea* a biohorizon *Ludwigia* spp. with a subquadratic whorl section predominate; however, in several specimens, the ventral shoulder is rounded. In contrast, ammonites of the morphogenus *Brasilia* are comparatively rare. Most specimens of *Ludwigia* spp. correspond to the "Artengruppe der *L. murchisonae* (Sowerby)" ("species-group of *L. murchisonae* (Sowerby)") of Rieber (1963: 53) which he defined as follows: The primary ribs divide into two or sometimes three secondaries in the area between the umbilical edge and mid-flank. The primaries are prorsiradiate, whereas the secondaries are strongly rursiradiate just from the diverging point onwards or immediately distal from this position. Towards the ventromarginal shoulder, the ribs become slightly elevated.



**Figure 7. (1a–5)** *Staufenia latiumbilicus* (Quenstedt) [M and m]. Southern slope of the Wochenberg hill; Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. **1:** SMNS 70640/11 ([M], bed 3; **2:** SMNS 70640/12 [m], bed 3; **3:** SMNS 70640/13 [m], bed 4; **4:** SMNS 70640/14 [M], bed 4; **5:** SMNS 70640/15 [M], bed 5. Asterisk marks beginning of bodychamber. Scale bars: Figs 1.1a, b: 5 cm; Figs 2–5: 3 cm.



Figure 8. (1a, b) Ludwigia aff. crassa Horn [M], St-B 5, SMNS 70640/16. (2a, b) L. armipotens (Buckman) [M], St-B 5, SMNS 70640/17. (3a-4b) Staufenia latiumbilicus (Quenstedt) [m], St-B 5; 3: coarsely ribbed, evolute variety, SMNS 70640/18; 4: SMNS 70640/19. (5a, b): S. latiumbilicus (Quenstedt) [M], giant-sized specimen, ?pathological, SMNS 70640/20. 1a-5b: southern slope of the Wochenberg hill; Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), latiumbilicus biohorizon. Asterisk marks beginning of bodychamber. Scale bars: Figs 1a-4b: 3 cm; Figs 5a, b: 10 cm.



**Figure 9.** (1–3, 5–7) *Staufenia latiumbilicus* (Quenstedt) [M], (1) SMNS 70640/21; (2) SMNS 70640/22; (3) SMNS 70640/23; (5) SMNS 70640/24; (7) SMNS 70640/25. (6) Paralectotype, original of *Ammonites discus latiumbilicus* Quenstedt, 1886, pl. 57, fig. 14, Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut der Universität Tübingen), GPIT-PV-61327, Schörzingen [= Wochenberg]. (4) *St. sehndensis* (Hoffmann) [M], holotype, original of *Ludwigia sehndensis* (Hoffmann, 1913, pl. 6, fig. 4) from Sehnde, Sehndensis Subzone, Geowissenschaftliches Museum der Universität Göttingen no. 73226 (459-78). 1–3, 5, 7: southern slope of the Wochenberg hill. 1–3. 5–7 Achdorf Formation, St-B 5; Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 10. (1a–2b)** *Staufenia latiumbilicus* (Quenstedt) [M]. **(1a,b)** Lectotype, original of *Ammonites discus latiumbilicus* Quenstedt (1886, pl. 57, fig. 8), St-B 3–5, Wochenberg, Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut Tübingen), GPIT-PV-6132. **(2a, b)** St-B 5, SMNS 70640/26. **1–2:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 11. (1a–6b)** *Staufenia discoidea* (Quenstedt) α. **(1)** [M], SMNS 70640/27, **(2)** [m], SMNS 70640/28, **(3)** [m], SMNS 70640/29, **(4)** [m], SMNS 70640/30, **(5)** [M], SMNS 70640/31. **(6)** Lectotype of *Ammonites discoideus* Quenstedt, 1886, pl. 58, fig. 3, SMNS 70640/32 [plaster cast; original in the Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut der Universität Tübingen), GPIT-PV-61330], Schörzingen [= Wochenberg]. **1a–5:** St-B 6, southern slope of the Wochenberg hill. **6:** St-B 6–8b. **1a–6b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 12. (1–3b)** *Staufenia discoidea* (Quenstedt) a [M], St-B 6. **(1)** SMNS 70640/32, **(2)** SMNS 70640/33, **(3)** SMNS 70640/34. **(4a, b)** *Brasilia howarthi* (Géczy) [M], St-B 6, SMNS 70640/35. **(5)** *Ludwigia subtuberculata* Rieber [m], St-B 7, SMNS 70640/36. **(6a, b)** *L. murchisonae* (Sowerby) [M], St-B 7, SMNS 70640/36. **(7a, b)**: *L. tuberata* (Buckman) [M], St-B 6, SMNS 70640/37. **1–7b**: southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* a biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 13.** (1–6) *Staufenia discoidea* α (Quenstedt). (1) [M], almost complete adult specimen, St-B 8b, SMNS 70640/38. (2) [m], almost complete specimen, with proximal part of apophysis, St-B 8a, SMNS 70640/39. (3) [M], smooth nucleus, St-B 8a, SMNS 70640/40. (4) [M], ribbed nucleus, St-B 8b, SMNS 70640/41. (5) [m], complete with apophysis, St-B 8a, SMNS 70640/42. (6) [m], coarsely ribbed variety, St-B 8b, SMNS 70640/43. 1a–6: southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 14. (1a, b)** *Ludwigia armipotens* (Buckman) [M], St-B 8a, SMNS 70640/44. **(2a, b)** *L. tuberata* Buckman [M], St-B 8a or 8b, SMNS 70640/45. **(3a, b)** *Staufenia discoidea* α (Quenstedt) [M], St-B 8a, SMNS 70640/99. **1a–3b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 15.** (1a, b) *Ludwigia depilata* (Buckman) [M], St-B 8a, SMNS 70640/46. (2a–4b) *L. subtuberculata* Rieber [m], St-B 8a. (2) SMNS 70640/47, (3) SMNS 70640/48. (4) SMNS 70640/49. (5a, b) *Brasilia elmii* (Géczy) [M], St-B 8a, SMNS 70640/50. 1a–5b: Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* a biohorizon. Asterisk marks beginning of bodychamber. Scale bars: Fig. 1: 5 cm; Figs 2–5: 3 cm.



Figure 16. (1a, b) Ludwigia armipotens (Buckman) [M], St-B 8a, SMNS 70640/51. (2) L. reflua (Buckman) [M], St-B 8b, SMNS 70640/52. (3a, b) Brasilia howarthi (Géczy) [M], St-B 8b, SMNS 70640/53. (4a, b) B. falcatiformis (Géczy) [M], St-B 8a, SMNS 70640/54. ( (5a, b): L. murchisonae (Sowerby) [M], St-B 8b, SMNS 70640/55. 1a–5b: Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 17. (1)** *Ludwigia reflua* (Buckman) [M], SMNS 70640/71. **(2)** *L. murchisonae* (Sowerby), SMNS 70640/72. **(3)** *Brasilia baldii* (Géczy) [M], SMNS 70640/94. **(1–3)** Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8b, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

After forming a very gentle forwardly bended curve, the coarse ribs end abruptly near the ventromarginal edge, so that a relatively broad, smooth band is developed in the area between the ventromarginal edge and the keel.

Ludwigia tuberata Buckman, 1904 [in Buckman 1887-1907] (Figs 12.7a, b; 13.2a, b) has the broadest whorl section and the coarsest ribbing of all Ludwigia specimens of the discoidea  $\alpha$  biohorizon. In the inner whorls, the diverging points of the ribs bear shovel-like thickenings. The bulk of the Ludwigia specimens of this biohorizon represent L. armipotens (Buckman, 1904 [in Buckman 1887–1907]) and L. reflua (Buckman, 1899 [in Buckman 1887-1907]). Both taxa share a prominent, falcate ribbing on the inner and median whorls and a smooth band along the blunt keel. L. armipotens (Figs 14.1a, b, 16.1a, b) shows an almost quadratic whorl section, whereas in L. reflua (Figs 16.2, 17.1a, b) the ventral margin is well-rounded. L. murchisonae perrotae Géczy, 1967 is indistinguishable from L. reflua. Specimens with a more slender, high-ovale to subquadratic whorl section and a weak ribbing are assigned to L. murchisonae (Sowerby) (Figs 12.6, 17.2). One of the nuclei (Fig. 16.5a, b) corresponds exactly to the inner whorls of the holotype of L. murchisonae (Sowerby, 1827) (plaster cast SMNS 70640/73). Several large specimens (Figs 15.1a, b) correspond better to L. depilata (Buckman, 1925 [in Buckman 1909–1930]). All microconchiate specimens of Ludwigia spp. are assigned here to L. subtuberculata Rieber, 1963 (Figs 12.5, 15.2a-4b). Morphologically, they are quite uniform and only differ from one another by their quadratic or subquadratic whorl section. The sculpture of the phragmocone varies between strongly and weakly ribbed.

Specimens showing a high and slender whorl section are assigned to *Brasilia*. They vary in the shape of the venter (rounded to quadratic/subquadratic), the strength of the ribbing and in their involution. A relatively coarsely ribbed *Brasilia* (Fig. 17.3a, b) with a rounded venter is assigned to *B. baldii* (Géczy, 1967). *B. theobaldi* (Géczy, 1967) (SMNS 70640/95) differs from *B. baldii* by a slightly weaker ribbing. Specimens showing weakly convex flanks with a subquadratic whorl section and a wide umbilicus are here assigned to *B. falcatiformis* (Géczy, 1967) (Fig. 16.4a, b). Two of our specimens are assigned to *B. elmii* (Géczy, 1967) (Fig. 15.5a, b). *B. howarthi* (Géczy, 1967) (Figs 12.4a, b, 16.3a, b) is extremely lanceolate and involute.

#### 4.4.3. discoidea β biohorizon

#### Genus Staufenia Pompeckj, 1906

All *Staufenia* specimens from this biohorizon represent *St. discoidea*  $\beta$ . In contrast, Rieber (1963: 14) assigned involute specimens from the uppermost layer of the Staufensis-Bank (St-B 8c) to *St. staufensis* (Oppel). This is seems plausible if only juveniles are considered (Fig. 18.2, 5, 6, 8). In the adults, however, the very narrow umbilicus of the inner whorls becomes rapidly wider on the median whorls (Fig. 18.1, 3–4), so that *St. discoidea*  $\beta$  represents a morphologically and chronologically intermediate form linking *St. discoidea*  $\alpha$  and *Staufenia staufensis* (Fig. 21). Most macro-

conchs are only weakly sculptured in the juvenile stage (Fig. 18.1–4, 6), and coarse-ribbed nuclei (Figs 18.7–18.8) are much rarer than in the *discoidea* a biohorizon below. The narrowing of the umbilicus seen in the evolutionary lineage from *Staufenia latiumbilicus* to *Staufenia staufensis* is associated with a gradual simplification of the suture line. This trend culminates in the very simplified suture of *Staufenia staufensis* (compare Rieber 1963, text-figs 17g, 17i, 19, 21).

From the *discoidea*  $\beta$  biohorizon, we recovered only a single, weakly sculptured microconchiate specimen of *St. discoidea*  $\beta$  (Fig. 18.5).

#### Genera Ludwigia Bayle, 1878 and Brasilia Buckman, 1899 [in Buckman 1887–1907]

Specimens of *Ludwigia* spp. from the *discoidea*  $\beta$  biohorizon generally exhibit a more slender whorl section than those from the *discoidea*  $\alpha$  biohorizon. Specimens assignable to the genus *Brasilia* are still rare.

*L. reflua* (Buckman, 1899 [in Buckman 1887–1907]) (Fig. 20.4a, b) ranges up to the *discoidea* β biohorizon. The specimens determined in open nomenclature as *L.* aff. *murchisonae* (Sowerby) (Figs 19.1a, b, 19.4a, b) differ from typical *L. murchisonae* in their slightly stronger ribbing (see *L. murchisonae* in Buckman 1887 [in Buckman 1887–1907], pl. 3, figs 1, 2). *L. gradata* Buckman, 1904 [in Buckman 1887–1907] (Figs 19.3a, b, 20.3a, b) is weakly ribbed and exhibits an even more slender whorl section than *L.* aff. *murchisonae*. *L. gradata* might be alternatively assigned to *Brasilia*; the differentiation between both genera is somewhat subjective. An evolute specimen with a rounded venter and a consistently coarse ribbing with shovel-like appearance in the bifurction points, is assigned to *L. fueloepi* Géczy, 1967 (Fig. 19.2a, b).

Ammonites of the genus *Brasilia* from the *discoidea*  $\beta$  biohorizon are represented by *B. bradfordensis* (Buckman, 1887) [in Buckman 1887–1907] (Fig. 20.2a, b) and *B. elmii* (Géczy, 1967) (SMNS 70640/96).

#### Genus Planammatoceras Buckman, 1922 [in Buckman 1909–1930]

A single, strongly weathered specimen (Fig. 20.1) is determined as *Planammatoceras* aff. *planinsigne* (Vacek, 1886). It differs from the lectotype of *P. planinsigne* by having weakly spinose diverging points of the ribs positioned higher on the flanks. In consequence, these nodes are arranged directly along the umbilical seam.

# 5. Revision of Quenstedt's (1886) ammonites from the Achdorf Formation of the Wochenberg hill or from Schörzingen

Quenstedt (1886) not only mentioned the Wochenberg hill itself but also the nearby village Schörzingen as finding localities of some ammonites listed below. Since the Achdorf Formation is not present within the village of Schörzingen, the specimens labeled with "Schörzingen" must either originate from the western or from the southern hillside of the



Figure 18. (1a-8) Staufenia discoidea (Quenstedt) β [M], St-B 8c, Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* β biohorizon. (1) SMNS 70640/56, (2) SMNS 70640/57, (3) SMNS 70640/58, (4) SMNS 70640/100, (5) SMNS 70640/59. (6) SMNS 70640/60. (7) SMNS 70640/61, coarsely ribbed variety.
(8) SMNS 70640/62, weakly ribbed variety. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 19. (1a, b, 4a, b)** *Ludwigia* aff. *murchisonae* (Sowerby) [M], **(1)** SMNS 70640/63, **(4)** SMNS 70640/64. **(2a, b)** *L. fueloepi* (Géczy) [M], SMNS 70640/65. **(3a, b)**. *L. gradata* Buckman [M], SMNS 70640/66. **1a–4b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8c, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* β biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 20. (1)** *Planammatoceras* aff. *planinsigne* (Vacek) [M], SMNS 70640/67. **(2a, b)** *Brasilia bradfordensis* (Buckman) [M], SMNS 70640/68. **(3a, b)** *Ludwigia gradata* Buckman [M], SMNS 70640/69. **(4a, b)**: *L. reflua* (Buckman) [M], SMNS 70640/70. **1a–4b:** Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8c, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea β biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

Wochenberg. All specimens originate from the Murchisonae Subzone of the Murchisonae Zone (Upper Aalenian).

 
 Table 1. Revision of Quenstedt's (1886) ammonites from the Achdorf Formation of the Wochenberg hill or from Schörzingen.

Original name in	Locality	Revised name and	Biohorizon
Quenstedt (1886)		nomenclatorial status	
A. discus	Wochenberg	St. latiumbilicus	latiumbilicus
latiumbilicus, p. 462,		(Quenstedt), lectotype	
pl. 57, fig. 8		(designated herein)	
A. discus	Schörzingen	St. latiumbilicus	latiumbilicus
latiumbilicus, p. 464,		(Quenstedt),	
pl. 57, fig. 14		paralectotype	
A. discoideus, p. 466,	Schörzingen	St. latiumbilicus	latiumbilicus
pl. 58, fig. 5		(Quenstedt)	
A. discoideus, p. 465,	Schörzingen	St. discoidea	discoidea α
pl. 58, fig. 3		(Quenstedt), lectotype,	
		selected by Hoffmann	
		(1913)	
A. discus Zieten, p.	Wochenberg	Staufenia discoidea	discoidea α
462, pl. 57, fig. 7		(Quenstedt)	
Ammonites discus	Wochenberg	Staufenia discoidea	discoidea α
Zieten, p. 461, pl. 57,		(Quenstedt)	
fig. 6			

# 6. Bio-/chronostratigraphy and correlation

#### 6.1. Bio-/chronostratigraphy

In our stratigraphical analyses, we focus on the beds of the Achdorf Formation and the directly overlying Sowerbyi-Oolith of the Wedelsandstein Formation.

# Bifidatum Subzone (Opalinum Zone, Lower Aalenian)

#### crassicostatum biohorizon

The Untere Wilflingen-Bank contains the *crassicostatum* biohorizon. Typical ammonites of this horizon are the coarseribbed *L. crassicostatum* along with *L. goetzendorfense* [formerly misidentified as *L. "comptum"*] and numerous morphological varieties. For a distinction from the older *uncinatum* biohorizon we refer to Dietze et al. (2021a). In the *evolutum* biohorizon, the graphoceratids are markedly smaller and mostly weaker ribbed than those of the *crassicostatum* biohorizon (Dietze et al. 2021b).

#### viallii biohorizon

The herein newly introduced viallii biohorizon of the Wochenberg hill was detected in the c. 1.7 m thick Obere Wilflingen-Bank. Its ammonite fauna is transitional between the ammonite fauna of the crassicostatum biohorizon (Rieber 1963) and that of the subfalcatum biohorizon (Dietze et al. 2021b). It yields ammonites of the genera Leioceras and Ancolioceras as well as transitional forms linking both morphogenera. L. goetzendorfense and L. striatum which first appeared in the crassicostatum biohorizon are now accompanied by L. evertens and L. capillare. The name-bearing species of the viallii biohorizon, A. viallii, is closer to Ancolioceras and hence assigned to this morphogenus. The morphospecies A. citaae, A. aff. subacutum,

A. krymholzi and A. noszkyi are already present in the viallii biohorizon, but become predominant in the younger sub-falcatum biohorizon of the Haugi Subzone.

The ammonite fauna of the crassicostatum biohorizon is more uniform than that of the viallii biohorizon. It is dominated by L. goetzendorfense (= L. comptum sensu Rieber 1963) with several extreme morphological varieties (see above and Rieber 1963). In comparison, the ammonite fauna of the viallii biohorizon looks much less uniform; approximately half of the ammonite fauna is represented by Ancolioceras, the other half by Leioceras (Figs 4, 5). The Tethyan genus Tmetoceras is only recorded from the crassicostatum biohorizon, but not yet from the viallii biohorizon. In the evolutum biohorizon described from the middle Swabian Alb relatively small-sized specimens of L. evolutum with some intraspecific variation predominate. L. evolutum itself is not present in the viallii biohorizon, but A. citaae exhibits some resemblance to L. evolutum var. comptocostosum (Dietze et al. 2021a, pl. 24, fig. 1). Apart from its coarser ribbing, L. evertens resembles L. evolutum var. costate (Dietze et al. 2021a, pl. 24, fig. 4). Dietze et al. (2021a) suspected that the evolutum biohorizon was younger than the crassicostatum biohorizon (Fig. 20). However, this can neither be verified nor falsified in the Wochenberg section, since no ammonites were recorded from the 3.6 m thick interval between the crassicostatum and the viallii biohorizon. In the viallii biohorizon, Leioceras spp. is still abundant; such morphologies become extremely rare in the subfalcatum biohorizon, where they are mostly replaced by Ancolioceras krymholzi, A. subfalcatum and A. subacutum. Additionally, in the subfalcatum biohorizon the first representatives of Ludwigia and questionable Staufenia spp. appear (Dietze et al. 2021b).

#### Haugi Subzone (Murchisonae Zone, Upper Aalenian)

The Haugi Subzone was not recorded at the Wochenberg hill. However, it is quite possible that sediments of this age locally occur, such as the calcareous marls below the "Sehndensis-Knollenlage" ("Sehndensis nodular layer") which were not studied in detail by us or a 0.8 m thick alternation of limestones and marly limestones which correspond to the questionable Sinon-Bank sensu Rieber. Rieber (1963) reported "Staufenia" sinon from this bed at the Wochenberg hill.

#### Murchisonae Subzone (Murchisonae Zone, Upper Aalenian)

#### latiumbilicus biohorizon

This biohorizon (beds St-B 4–5) is exclusively characterized by its index ammonite *Staufenia latiumbilicus*. Ammonites of the genus *Ludwigia* are extremely rare and do not contribute to the recognition of this biohorizon. A differentiation towards the next older described *opalinoides* biohorizon is rather simple, since in the latter the genus *Ancolioceras* predominates (see Horn 1909; Rieber 1963),

Concavum	Formosum	yet to be worked out	?Geisingen, Ringsheim, Wutach
	Concavum	cavatum	Zollernalb (Wannenmacher et al. 2021), ?Kappishäusern, ?Metzingen [Rieber 1963]
Bradfordensis		decipiformis	Geisingen (Dietze et al. 2014)
	Gigantea	geisingensis	Geisingen, Öfingen (Dietze et al. 2014)
		gigantea sensu Contini	Geisingen (Dietze et al. 2014), Wutach (condensed)
	Bradfordensis	yet to be worked out	Aalen [Quenstedt 1886, Rieber 1963], Kuchen, Geislingen, Wutach (condensed)
		staufensis	Swabian Alb, Wutach [Quenstedt 1886, Horn 1909, Rieber 1963], Geisingen , Ringsheim
MurchisonaeH	Murchisonae	discoidea β	Wochenberg, Plettenberg [Quenstedt 1886, Rieber 1963]
		discoidea α	Wochenberg, Gosheim
		latiumbilicus	Wochenberg [Quenstedt 1886, Rieber 1963], ?Gosheim
		yet to be worked out	Gosheim
	Haugi	yet to be worked out	Gosheim, Geisingen, Aalen
		opalinoides	Geisingen, Wutach [Horn 1909, Rieber 1963], Wochenberg [Rieber 1963]
		subfalcatum	Aichelberg [Dietze et al. 2021b]
Bifidatum [ex Comptum] Opalinum Opalinum		viallii	Wochenberg [here], ?Gosheim
	Bifidatum [ex Comptum]	evolutum	Aichelberg area [Dietze et al. 2021a]
		crassicostatum	Swabian Alb, Wutach [Rieber 1963], N Franconian Alb [Dorn 1935]
		uncinatum	Aichelberg area [Dietze et al. 2021a]
		bifidatum/rieberi	Aichelberg area [Dietze et al. 2021a]
	Opalinum	hansrieberi	Swabian Alb [Ohmert 1993 Dietze et al. 2018, 2021a]
		opaliniforme	Swabian Alb [Ohmert 1993, Dietze et al. 2021a]
	Opainfulfi	dilucidum <sup>1</sup>	Swabian Alb [Dietze et al. 2021a], Franconian Alb [Schulbert 2001]
	opalinum <sup>1</sup>	Swabian Alb [Dietze et al. 2021a], Wittnau [Ohmert 1993]	

#### Table 2. Biohorizons in the Aalenian of SW Germany. Those which are recorded at the Wochenberg hill are shaded in dark gray.

Remark1: the opalinum and dilucidum biohorizons are recorded in the nearby claypit at Weilen unter den Rinnen.

whereas large-sized specimens of the lanceolate *Staufenia latiumbilicus* dominate in the *latiumbilicus* biohorizon. However, we want to point out that at least one or two further still undescribed biohorizons are developed between the *opalinoides* and the *latiumbilicus* biohorizon in the Aalenian of SW Germany (Aalen, Gosheim, Geisingen) (Table 2).

#### discoidea α biohorizon

The discoidea a biohorizon (beds St-B 6–8b) is characterized by its name giving species *Staufenia discoidea* a together with ammonites of the genus *Ludwigia*, which Rieber (1963) classified as "Artengruppe der *Ludwigia* (*L.*) *murchisonae*" ("species group of *Ludwigia* (*L.*) *murchisonae*"). The discoidea a biohorizon is distinguishable from the next older *latiumbilicus* biohorizon by yielding markedly more involute specimens of *Staufenia* accompanied by various *Ludwigia* spp. of the "Artengruppe der *L. murchisonae*" sensu Rieber (1963) and earliest representatives of *Brasilia*; the latter two ammonite groups are still absent in the *latiumbilicus* biohorizon of SW Germany.

#### • discoidea β biohorizon

The discoidea  $\beta$  biohorizon (Schicht St-8b) is characterized by the index species *Staufenia discoidea*  $\beta$  and an accompanying fauna containing *Ludwigia* spp., which Rieber (1963) summarized as the "Artengruppe der *Ludwigia* (*L.*) murchisonae". The discoidea  $\beta$  biohorizon mainly differs from the next older discoidea  $\alpha$  biohorizon by the evolutionary state of the genus *Staufenia*; *St. discoidea*  $\beta$  is morphologically transitional between *St. discoidea*  $\alpha$  and the younger, extremely involute *St. staufensis. Ludwigia* specimens of the *discoidea*  $\beta$  biohorizon have more slender whorl sections and a better rounded venter; a trend which continues up to *Brasilia* spp. of the Bradfordensis Zone. In the next younger *staufensis* biohorizon (Rieber 1963; Dietze et al. 2017), the ammonites of the genus *Staufenia* with its index *St. staufensis* are still more involute than those of the *discoidea*  $\beta$  biohorizon. The "Artengruppe der *L. murchisonae* sensu Rieber" is later replaced by the "Artengruppe der *L. bradfordensis*" sensu Rieber (1963); however, numerous transitional forms exist.

#### Bradfordensis Zone (Upper Aalenian)

Beds of the *staufensis* biohorizon (Dietze et al. 2017) have not been recorded at the Wochenberg hill. Rieber (1963) interpreted nuclei of *Staufenia* from the *discoidea*  $\beta$  biohorizon as belonging to *St. staufensis*. This erroneously implied the presence of the Bradfordensis Zone and is corrected here. No beds of the Bradfordensis Zone have been recorded from the Wochenberg hill.

#### Concavum Zone (Upper Aalenian)

Rieber (1963) reported the "Concava-Bank" near the Wochenberg hill, although he could not find any ammonites in this bed. The "Concava-Bank" most likely represents the Concavum Zone, as it is the case in other parts of the western Swabian Alb (Rieber 1963; Wannenmacher et al. 2021).

#### Discites Zone (Lower Bajocian)

From a bed following immediately below the "Sowerbyi-Oolith-Knollenlage" ["Sowerbyi-oolith nodular layer"], Rieber (1963) recorded the ammonite genus *Hyperlioceras*. A fragmentary Sonninia sp. labelled as originating from the Sowerbyi-Oolith of the Wochenberg hill is stored in the palaeontological collection of Tübingen University. These two finds clearly indicate that the Sowerbyi-Oolith in the vicinity of the Wochenberg hill belongs to the Discites Zone, as it is the case in all other studied places of the western Swabian Alb (Rieber 1963; Dietze et al. 2019).

#### 6.2. Correlation within Germany

North Germany: Hoffmann (1913) described a rich ammonite fauna from the Aalenian of Sehnde near Hannover. The Sehndensis-Subzone of North Germany includes time-equivalent strata of the *latiumbilicus* biohorizon, and the Discoidea-Subzone strata of the *discoidea*  $\alpha$  and  $\beta$  biohorizons.

SW Germany: The crassicostatum biohorizon is widespread in the western Swabian Alb (Rieber 1963). A set of beds occurring a few metres above the (Untere) Wilflingen-Bank in a section at the Wilflinger Steige near Gosheim contain ammonites which could represent the viallii biohorizon; their description is still in progress. In 2020, the discoidea a biohorizon was recorded by the first author for the first time in Gosheim within a c. 1 m thick, probably only locally developed set of arenaceous limestone beds which were temporarily exposed along the connectiong road to the industrial area Sturmbühl. The somewhat deeper occurring "Schichten mit Staufenia sehndensis" ["beds with Staufenia sehndensis"] at Gosheim (Rieber 1963; Dietze 1989a, b), which are very rich in ammonites and shell detritus, are slightly older than the latiumbilicus biohorizon. Since bed-by-bed collections from further localities of the Swabian and Franconian Alb as well as from the Wutach area and the Upper Rhinegraben valley are still lacking, further correlations at the level of biohorizons are impossible.

#### 6.3. Correlation outside Germany

France (Franche-Comté): Contini (1969, Tableau I) correlated the ammonite successsion of the French Jura Mountains with the successions of North Germany (Hoffmann 1913) and SW-Germany (Rieber 1963). This correlation was later adopted and revised by Contini et al. (1997, Tableau Va) in a rather confusing way. Different zonal schemes were used for the so-called "biome franco-germanique" [partly inluding the French Jura Mountains] on the one hand and the Submediterranean and Subboreal provinces on the other. Most strangely, the discoidea-Horizont sensu Rieber was totally ignored within these "horizons" of the "biome franco-germanique". The stratigraphic position of the "Horizon à Sehndensis" [biome franco-germanique] was placed between the "Horizon à Obtusiformis" and the "Horizon à Murchisonae" [of the Submediterranean/ Subboreal provinces] in Tableau Va; however, in the corresponding text it was explained that the faunas of the "Horizon à Sehndensis" in the French Jura Mountains and

in SW Germany [biome franco-germanique] are identical with the fauna of the "Horizon à Obtusiformis" [Submediterranen/Subboreal provinces].

This is why we prefer the more consistent and reproducable subdivision of Contini (1969) for our correlation between SW Germany and the French Jura Mountains. Contini's "Horizon à Staufenia sehndensis" with *St. sehndensis* und *Ludwigia obtusiformis* is slightly older than the *latiumbilicus* biohorizon at the Wochenberg hill, where *L. obtusiformis* has not been recorded yet. At Gosheim, only a few kilometres south of the Wochenberg hill, *L. obtusiformis* is recorded and co-occurs with smaller-sized *St. "sehndensis"* (Dietze 1989a, p. 125 figure bottom right, 1989b, p. 172 top left); hence, we suspect these beds correlate with the French Horizon à Sehndensis. The *discoidea* a und *discoidea*  $\beta$  biohorizons correspond to the Horizon à Murchisonae of the French Jura Mountains.

South England (Dorset): Despite of numerous previous studies (Buckman 1887-1907; Callomon and Chandler 1990; Chandler 1982, 1997), a correlation between SW Germany and S England remains problematic. The main reasons are that Staufenia discoidea and St. staufensis do not occur in S England and the corresponding faunas with Ludwigia spp. from England are generally more weakly sculptured and more rounded in ventral aspect than those of SW Germany (Chandler et al. 2012). The faunal horizon of Ludwigia obtusiformis with St. sehndensis, L. obtusiformis and Ancolioceras spp. (Chandler 1982, 1997; Callomon and Chandler 1990, 1997) must be slightly older than the latiumbilicus biohorizon based on the same arguments as explained above for our correlation with the French Jura Mountains. For a correlation of the faunal horizon of L. patellaria only its index L. patellaria can be used (Callomon and Chandler 1990). Since specimens of Ludwigia are extremely rare in the latiumbilicus biohorizon of SW Germany, it is impossible to decide whether both horizons could be time-equivalent or which one is the older. Possibly, the latiumbilicus biohorizon is the younger one of the two, since the few Ludwigia specimens already show a smooth band along the keel; this is not the case in L. obtusiformis. The discoidea α und β biohorizons correlate with the faunal horizon of L. murchisonae. The newly introduced viallii biohorizon is either slightly older or coeval with the comptocostosum horizon of Chandler and Callomon (2010).

**Scotland (Isle of Skye):** Morton and Hudson (1995) divided the rock succession at the type locality of *Ammonites murchisonae* Sowerby, 1827 – the type species of *Ludwigia* Bayle, 1878 – into the same faunal horizons as in South England (Callomon and Chandler 1990). The beds 0.7-0.11 of the Ollach Sandstone Member were assigned to the Murchisonae Subzone, with the two faunal horizons of *L. patellaria* and *L. murchisonae*. These beds correlate with the *latiumbilicus, discoidea* a und *discoidea*  $\beta$  biohorizons in the Wochenberg section.

Switzerland (Central Swiss Jura): Christ (1999, 2000) divided the rock in the central Swiss Jura Mountains into a succession of several ammonite faunas; however, his study is merely hypothetical since it is mostly based on



Staufenia latiumbilicus

**Figure 21.** Evolution of the genus *Staufenia* in the Upper Aalenian of the Swabian Alb. *Staufenia staufensis* originates from the Plettenberg hill (Dietze et al. 2017, pl. 4, fig. 7), all other ammonites from the Wochenberg hill. The *staufensis* biohorizon is not present at the Wochenberg hill due to Quaternary erosion. Scale bar: 3 cm.

imprecisely collected museum material (collection Lieb/ Bodmer). His fauna 6 "murchisonae und ssp." approximately correlates with the discoidea  $\alpha$  und  $\beta$  biohorizons.

In the Aalenian of **Luxembourg**, Sadki et al. (2020) divided the Murchisonae Subzone into biohorizons; however, the few specimens of *Ludwigia* spp. presented in their study do not allow a precise correlation. A high-resolution correlation with **further European regions** is impossible due to the lack of published data.

# 7. Discussion and conclusions

The evolution of the genus *Staufenia* is well-recorded in sections of the Wochenberg and nearby Plettenberg hills (Rieber 1963; Dietze et al. 2017, this study). Although time-equivalent populations show some morphological variation, this variation shifts continuously during evolution. Four evolutionary trends are observed through time (Fig. 21): (1) The umbilical width decreases. (2) The narrowing of the umbilicus is reinforced by a gradual change from a steep to an overhanging umbilical wall during ontogeny. (3) The strength of ribbing decreases and ribbing becomes restricted to earlier and earlier ontogenetic stages. (4)

The suture line becomes simplified. At least the first three evolutionary trends are closely related with each other and occur in many other highly variable ammonite genera. This phenomenon is well-known as "Buckman's rules of covariation" (see Monnet et al. 2015 for more details). Concerning the simplification of the suture line, there is no consistant correlation between complexity of the suture lines and water depth (Lemanis 2020). Therefore, this simplification must be an adaptation to other environmental conditions hardly decipherable without any autecological data.

But why are evolutionary trends in *Staufenia* appear to be continuous and targeted, whereas they are discontinuous and random in *Leioceras/Ancolioceras*? A possible reason could lie in the different distribution ranges of these genera. *Staufenia* is an endemic genus restricted to present-day Germany, E France and S England [only recorded there up to the Obtusiformis Subzone], whereas *Leioceras/Ancolioceras* had a much wider geographic distribution including the entire Tethyan realm. In the latter taxa, different environmental conditions (e.g. water temperature, food supply) in various parts of the distribution area might have led to different adaptations in the various populations. When such temporarily spatially isolated populations of *Leioceras/Ancolioceras* showing an onset of speciation later became reunified, e.g. in the course of a sealevel rise reconnecting neighbouring basins and thus allowing an interbreeding of their populations, this may have resulted in seemingly random developments.

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