Berliner paläobiologische Abhandlungen	10	361-371	Berlin	2009-11-11

Additional *Prionocyclus germari* (Reuss, 1845) (Cretaceous Ammonoidea, Upper Turonian) from NW Germany

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Abstract: The Upper Turonian index ammonite *Prionocyclus germari* is a rare species in NW Germany. To contribute to the knowledge of the distribution of this species, new finds from Lower Saxony are described. Surprisingly, these are characterized by the occurrence of inner and outer ventrolateral tubercles up to sizes of several cm, which make them differ from the north American populations of the Western Interior Seaway. *P. germari* seems to occur preferably in or close to swell settings together with a diverse associated invertebrate fauna. Time-equivalent beds in intra-shelf depressions are depleted of macrofauna.

Keywords: Ammonoidea, Upper Cretaceous, Upper Turonian, *Prionocyclus*, ecology

Zusammenfassung: Der oberturone Index-Ammonit *Prionocyclus germari* ist in NW-Deutschland selten. Daher werden hier einige neue Funde aus Niedersachsen beschrieben, um die geographische Verbreitung zu dokumentieren. Überraschenderweise unterscheiden sich die Funde durch innere und äußere Ventrolateral-knoten, womit sie sich vom Material des Western Interior Seaways unterscheiden. *P. germari* kommt bevorzugt nahe Intraschelf-Schwellen mit einer typischen begleitenden Makrofauna vor. Zeitgleiche Schichten in Intraschelf-Senken sind an Makrofauna verarmt.

Schlüsselwörter: Ammonoidea, Oberkreide, Oberturon, *Prionocyclus*, Ökologie

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1. Introduction

The collignoniceratid ammonite species *Prionocyclus germari* (Reuss, 1845) represents the end member of the Middle to Upper Turonian *Prionocyclus* lineage, which is particularly well documented from the USA (Kennedy et al. 2001). It is an index marker for the *P. germari* Zone, which is used to define the uppermost Turonian by ammonite stratigraphy in NW Germany, Bohemia and Tunisia (Čech 1989, Kaplan & Kennedy 1996, Robaszynski et al. 2000) as well as the Upper Turonian *germari* Zone in the USA (Cobban 2008). Although used for stratigraphic purposes, the number of recorded specimens from NW Germany is scarce and mainly limited to the lower parts of its nominal zone. From Westphalia, Kaplan (1988) described four records from several localities, and from the Wüllen section (Ernst et al. 1998), the species is also mentioned. From Lower Saxony, Schlüter (1872) mentioned three specimens. In the last years, several further findings occurred in Lower Saxony, which will be described here to contribute to the knowledge of its distribution. Furthermore, the material shows some peculiarities which suggest that the NW German stock may have experienced morphological individual characteristics which deviate from the North American material.

2. Regional geology and find localities

In the working area (Lower Saxony, Sachsen-Anhalt; Fig. 1), the lower Upper Cretaceous rocks are united in a number of formations, of which the Salder and the succeeding Erwitte formations include Upper Turonian strata (Fig. 2). The Salder Formations consists of white to grey hard and splintery limestone (pelagic nanno-fossil oozes mainly with calcareous dinoflagellate cysts, planktonic foraminifera and inoceramid debris) with rare intercalated detrital marl seams and marl beds (e.g. marl M_E) and volcanogenic marls (bentonites T_D, T_E, T_F). The succeeding Erwitte Formation is a well-developed marl/limestone alternation in its lower part (Grey and White Alternation, GWA) with white limestones as in the Salder Formation and silt-bearing grey marly limestone units, which are intercalated by thick (up to 150 cm) marls. A large amount of details on lithology, integrated stratigraphy and faunal characteristics is given by, e.g., Ernst et al. (1983), Niebuhr et al. (2000), Wiese et al. (2007a, b), Wiese & Kröger (1998) and Wood & Ernst (1998), and the reader is referred to these papers.

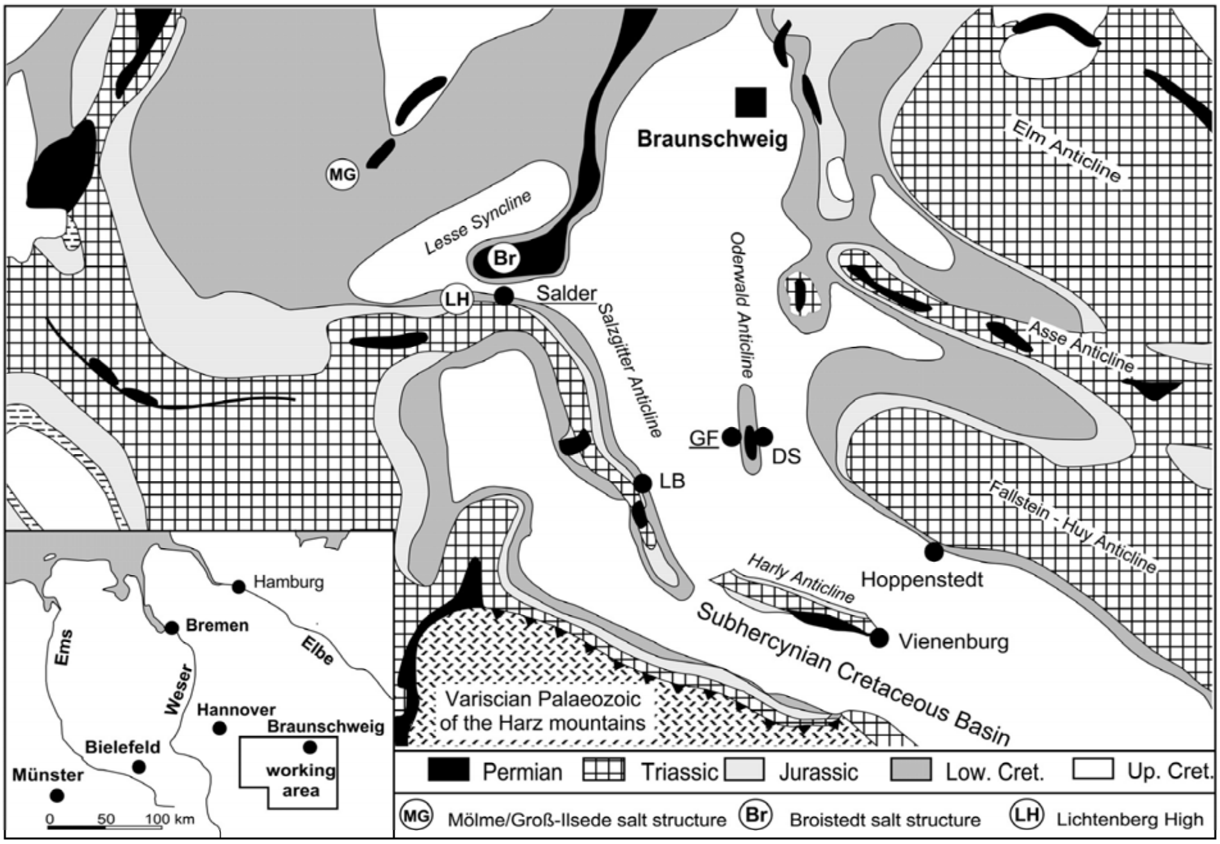
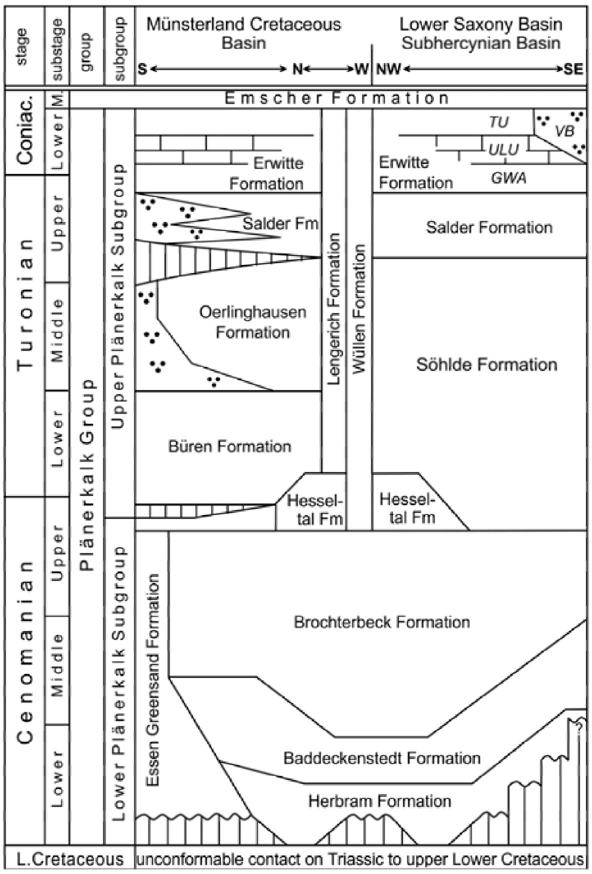


Fig. 1: Overview over the working area in Lower Saxony and Sachsen-Anhalt. Locations mentioned in the text are underlined. Abbreviations: **LB:** Liebenburg, **GF:** Groß-Flöthe, **DS:** Dorstadt.



The excellent stratigraphic framework with a number of event beds enables a safe orientation within the often monotonous white limestone. The interval considered and discussed here is particularly tightly fixed within this framework. It ranges from the bentonite T_F (ca. the base of the *Mytiloides scupini* inoceramid Zone) to the lowermost Erwitte Formation (comp. Fig. 3). The depositional area was laterally structured into intra-shelf swells (e.g. Groß-Flöthe) and depressions (e.g. Salzgitter-Salder), resulting in well-developed lateral facies variation (Fig. 3), as indicated by lithology and fauna.

Fig. 2: Lithostratigraphic framework of the Plänerkalk Group (Cenomanian to Lower Coniacian) in NW Germany. Abbreviations: **GWA:** Grey and White Alternation, **ULU:** Upper Limestone Unit, **TU:** Transitional Unit, **VB:** Vienenburg Member (for details see Niebuhr et al. 2007).

3. Systematic Account

Collignoniceratidae Wright & Wright, 1951
Collignoniceratinae Wright & Wright, 1951
Prionocyclus Meek, 1876

Type species: *Prionocyclus wyomingensis* Meek, 1876 (comp. Kennedy et al. 2001)

Prionocyclus germari (Reuss, 1845)

1845 *Ammonites Germari* Reuss: p. 22, pl. 7, fig. 10

1872 *Ammonites Germari* Reuss: Schlüter, p. 41, pl. 11, figs 15-17.

1988 *Prionocyclus germari* (Reuss, 1845): Kaplan, p. 37, pl. 3 figs 1-3, p. 43, pl. 6 fig 1.

2001 *Prionocyclus germari* (Reuss, 1845): Braunberger & Hall: p. 1125, pl. 3, figs 1-18.

2001 *Prionocyclus germari* (Reuss, 1845): Kennedy, Cobban & Landman, fig. 108A,B, D-F, figs 109-119, with comprehensive synonymy.

2000 *Prionocyclus germari* (Reuss, 1845): Robaszynski et al., p. 442, pl. 1, figs 7-8.

2003 *Prionocyclus germari* (Reuss, 1845): Kennedy, Phansalkar & Walaszczyk, p. 435, fig. 2.

2005 *Prionocyclus germari* (Reuss, 1845): Andrade, pl. 11, fig 2

Type: Lectotype is the original of Reuss, 1845, pl. 7, fig. 10, designated by Kennedy et al. (2001).

Material and stratigraphic provenance: 10 fragments and fragmentarily preserved specimens from the lower *scupini* Zone of NW Germany, deposited and registered in the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie: NsK 1-6 from the upper Salder Formation of Groß-Flöthe, NsK 6 and NsK 7 (cast of a mould) from the upper Salder Formation of Dorstadt, NsK 8 from the lowermost Erwitte Formation of Salzgitter-Salder, NsK-9 from the upper Salder Formation of Hoppenstedt and NwK 1 from the Wüllen Formation of Wüllen, Westphalia. Although mainly collected not in situ, NsK 1-9 unequivocally comes from above the *Micraster* Event (lower *scupini* Zone; comp. Fig. 3). The Wüllen specimen from the Hollekamp quarry is labeled “K6 + ca. 5,80 m, härtere Kalkbank, Wüllen, 3.4.89” by G. Ernst (comp. Ernst et al. 1998, p. 160, fig. 9) ca. 2 m above the *Hyphantoceras* Event.

Description: One fragmented juvenile (1/2 whorl, suggesting a diameter of ca. 25 mm, umbilical walls not preserved) shows a dense simple prorsiradiate ribbing (ca. 16 ribs/half whorl) that leads to inner and outer ventrolateral clavi. Secondary ribs are weaker in the umbilicolateral area but have same strength high upflank. The venter is not preserved. Due to the mode of preservation, an umbilical bulla is only observed in one main rib. In larger specimens (NsK 1; Pl. 1, Fig. E), coiling is evolute and the umbilical wall is steep. Whorl section is high oval in intercostal to polygonal in costal areas. From the umbilical shoulder, strong prorsiradiate ribs arise (ca. 10 per half whorl) that bear umbilical bullae in early growth stages, which migrate to a low flank position in middle growth stages. Secondary ribs are intercalated irregularly and bear no or only very weak umbilical bullae. With increasing size, ribbing can become somewhat flexuous in some specimens (Pl. 1, Figs. B, C). The bullae in the low flank position (Pl. 1, Fig. I) can shift slowly into elongated, bullate swelling at the umbilical shoulder in some specimens (Pl. 1, Figs. A-B), while in other the position in a low flank position is maintained (Pl. 1, Fig. J). All ribs terminate in well-developed inner ventrolateral slightly clavate tubercle. A low rib bends forward and links to weaker outer ventrolateral clavi. From there, ribbing forms an acute chevron on the almost flat venter, which has an elevated and serrated keel with serrations outnumbering the numbers of ribs significantly. After a size of ca. 50 - 55 mm (NsK1 & 3), the outer vetrolateral clavi progressively disappear. Specimen NsK-4 (Pl. 1, Fig. D) is poorly preserved but shows much finer ribbing and weaker secondary ribs that also bears much weaker inner ventrolateral tubercles and no outer row of tubercles is developed. Specimen NwK 1 from Wüllen (Pl. 1, Figs. A, B) is ca. 1/4 of a whorl. It shows the crenulated keel on an almost flat venter, the row of inner ventrolateral tubercles which form well-developed spines. The whorl section was subrectangular, and ribbing is comparatively weak.

Discussion: Kennedy et al. (2001) presented a revision of the American representatives of the genus *Prionocyclus*, and the material from NW Germany fits in the morphological variability of *P. germari* as documented on numerous figures (Kennedy et al. 2001, figs. 108A, B, D-F, figs. 109-119) with respect to ribbing, whorl section and involution. However, the persistence of outer ventrolateral tubercles up to a size of around 55 mm in the material from Lower Saxony represents a peculiarity, which is not recorded from any of the representatives of *Prionocyclus*. By this, it differs from the material described by Kennedy et al. (2001), where the outer ventrolateral clavi disappear at a size of 15 mm in those that they describe as robust forms. With this respect, the material here (e.g. specimen NsK 1; Pl. 1, Fig. E) shows strong reminiscence of *S. normalis* as figured by Wright (1979, p. 315, pl. 5, fig. 6a). However, the crenulated venter, indicative of *Prionocyclus*, clearly distinguishes the material presented here from the latter species. Kaplan (1988, pl. 5, figs. 4-6) figured 2 specimens as *S. normalis*, but in his description he recorded the occurrence of a crenulated keel. This is rather indicative of *Prionocyclus* instead of *Subprionocylcus*, which has ventral clavi in an approximate number of ribs (Wright et al. 1996, see also Wright 1979, p. 315, pl. 5, fig. 6a). Therefore, these specimens may also carefully be regarded as representatives of *Prionocyclus* and may or may not also represent *P. germari*.

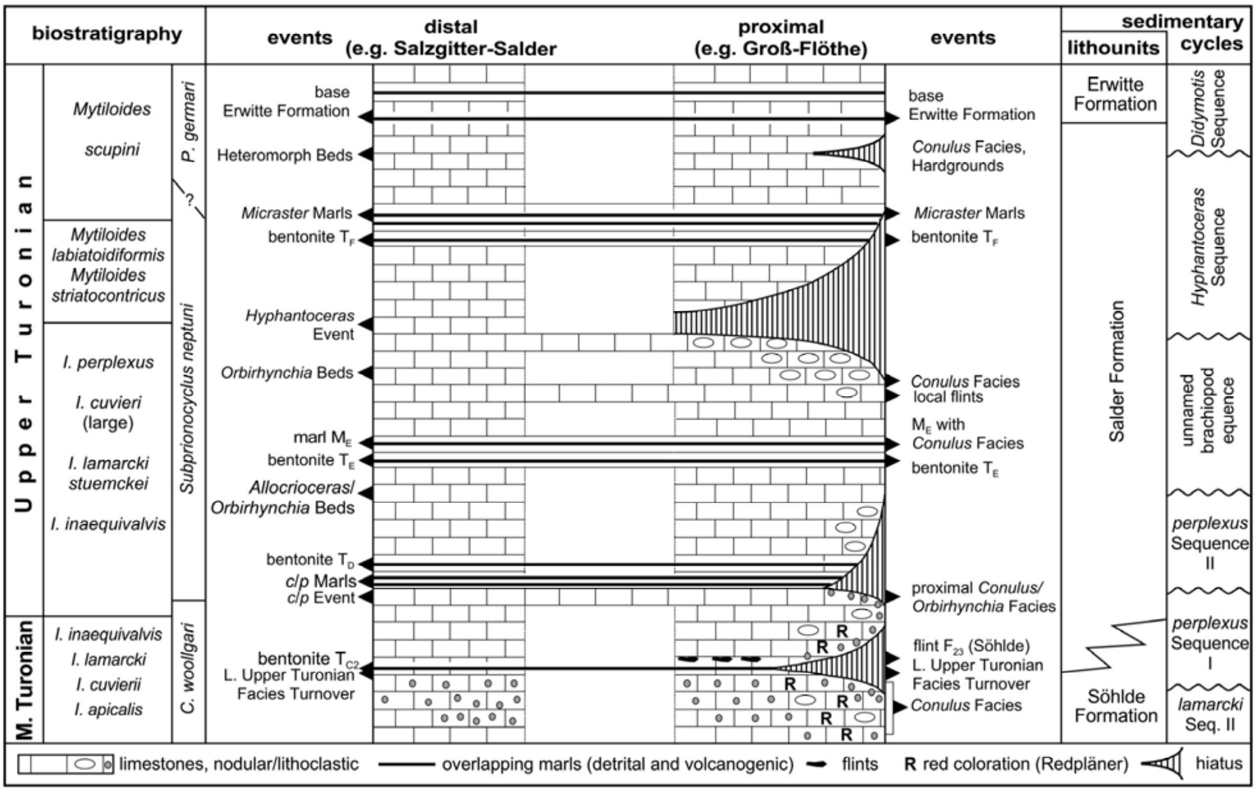


Fig. 3: Lateral lithostratigraphic relations within the upper Söhlde to lower Erwitte Formations in Lower Saxony and Sachsen-Anhalt with details of biostratigraphy and event stratigraphy. Synthesized after Ernst et al. (1979), Niebuhr et al. (2000) and own data.

Given the overall similarity of ribbing and the tubercles in a low flank position in context of a stratigraphic position well in the lower part of the *scupini* Zone, the fragmentary mould of an unidentified collignoniceratid of Horna & Wiese (1997, pl. 1, fig. e) of the uppermost Salder Formation of Hoppenstedt, Sachsen-Anhalt (NsK 9; here refigured on Pl. 1, Fig. G) is also referred to as *P. germari*. The specimen figured by Kaczorowski (2000: p. 245, figs. 3-4) as *P. germari* lacks the typical mode of straight prorsiradiate ribbing and any ventrolateral tubercles. Due to the indistinct figure of this poorly preserved fragment, it is not clear whether it represents a collignoniceratid at all. Based on the scarce finds from NW Germany, it is impossible to decide whether the occurrence of inner and outer ventrolateral tubercles up to a size of several cm justifies the separation of an independent species or whether this is merely an expression of a regional eco-phenotype. However, as the overall characteristics are in good accordance with the species concept of *P.*

germari (except from the development of the ventrolateral tuberculation), the herein described forms are referred to the latter taxon.

Regional Distribution and Stratigraphy: *P. germari* is rare in NW Germany. A single specimen has been figured by Schlüter (1872) from the upper "Scaphitenschichten" (= upper Salder Formation) of the vicinity of Groß-Döhren near Liebenburg (comp. Fig. 1). He mentions two further fragments from the area. Kaplan (1988) published four specimens from Westphalia, and the small collection presented here almost doubles the scarce numbers of records from NW Germany. The species is also recorded from Brazil, the USA, Canada, Angola, Tunisia, Spain, Czech Republic and India. The Polish occurrence is considered as a doubtful record.

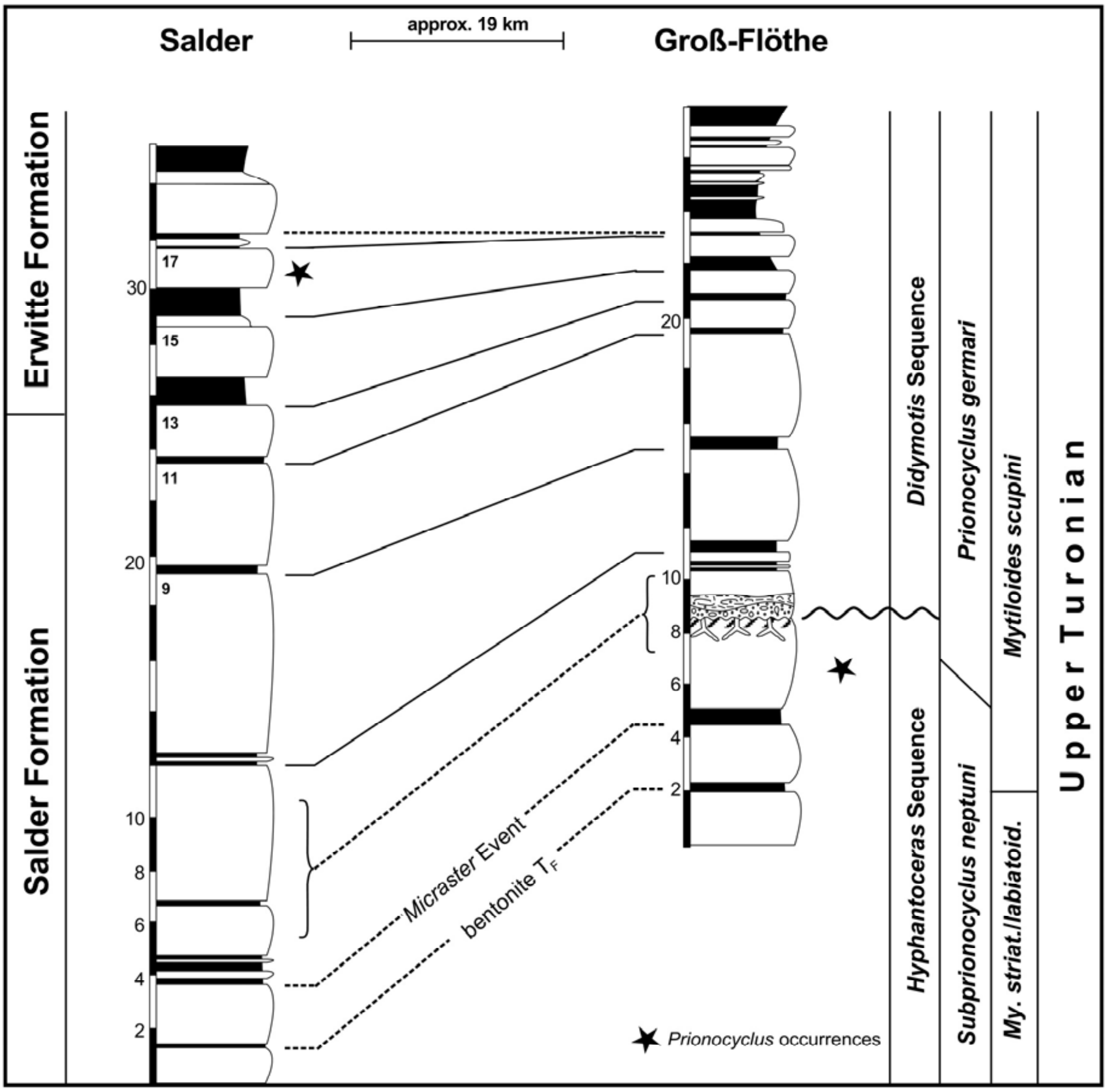


Fig. 4: Correlation between Salzgitter-Salder and Groß-Flöthe (after Wiese & Kröger 1998)

P. germari is used to define the terminal Upper Turonian ammonite zone in the standard ammonite zonation (comp. Kennedy et al. 2001). Assuming that the *S. normalis* of Kaplan (1988) are *P. germari*, the base of the *germari* Zone is located below the *Micraster* Marls and above bentonite T_F (Fig. 3). This fits also the situation in northern Spain, where Wiese (1997) reports *P. germari* from the base of the *scupini* Zone. In this case, the bases of the germari and scupini zones are approximate time-equivalents. As can be seen in the Bohemian Cretaceous Basin (Čech & Švábenická 1992), the upper limit of *P. germari* correlates roughly with the Turonian/Coniacian boundary interval. Within this context, it is problematical to define the upper Upper Turonian with a *germari* Zone in NW Germany (Kaplan & Kennedy 1996), because all records come exclusively from the lower part of its total range. Thus, the application and interbasinal correlation of total range zones (TRZ) of *P. germari* without any additional stratigraphic support by inoceramids or $\delta^{13}C$ correlations, bears potential for a stratigraphic miscorrelation of *germari* zones of the various regions. In Tunisia, Robaszynski et al (2000) distinguished an upper Upper Turonian *P. germari* TRZ as applied by Kaplan & Kennedy (1996), succeeded by a *Barroisiceras* cf. *tunetanum* Zone, which marks the lowermost Coniacian ammonite Zone of Robaszynski et al (2000). However, the first occurrence of the genus *Barroisiceras* is located well in the Upper Turonian (Summesberger & Kennedy 1996), and it might be possible that the *P. germari* does not occur throughout it stratigraphic range Tunisia. Instead, it appears that the occurrences might be restricted to the lower part of the *germari* TRZ and is expression of a short-termed incursion epibole (Wiese & Voigt 2002).

4. Discussion

Most of the material is derived from the abandoned Groß-Flöthe quarry (5 specimens) and the nearby Dorstadt section (2 specimens) of the Oderwald (Fig. 1). The Groß-Flöthe area represents the shallowest setting recognized in the lower *scupini* Zone of Lower Saxony so far (comp. Fig. 3, 4), and the fauna is characterized by elements of what is known as *Conulus* Facies (Galeritenschichten of Löscher 1912), which only develops in shallower settings of the Middle to Upper Turonian in Westphalia and Lower Saxony (see discussion in Wiese & Kröger 1998). Although a handful of specimens are far away from indicating clear trends, the occurrence of *P. germari* at Groß-Flöthe fits well in its distribution pattern as observed in Westphalia and Lower Saxony and for other collignoniceratids in general. As discussed by, e.g., Tanabe (1979), Tanabe et al. (1978) and Kaplan (1988, 1991), collignoniceratids avoided too distal settings or open marine settings, respectively but in NW Germany they can be shown to occur also in intra-shelf swell positions as indicated by the herein described specimens from Groß-Flöthe and Wüllen, Westphalia (Wiese & Kröger 1998, Ernst et al. 1998). The lateral variation of the ammonite facies from proximal to distal within Lower Saxony can be illustrated by the comparison of the lowermost *scupini* Zone (from the base of the *scupini* Zone to the top of the Salder Formation) between Groß-Flöthe (intra-shelf swell) and Salzgitter-Salder (intrashelf-depression; comp. Fig. 3). In Groß-Flöthe, *Hyphantoceras ernsti* Wiese 2000 as well as *Lewesiceras mantelli* (Wright & Wright, 1951), scaphitids and baculitids are fairly common, *P. germari* has been collected in several specimens, *Eubostrychoceras saxonicum* (Schlüter, 1875) is rare as are fragments of giant ammonites (estimated diameter up to 50 cm). While scaphitids and baculitids are ubiquitous elements of the upper water column irrespective of their distance from the coast (Westermann 1996), giant ammonites, *P. germari* and the frequent occurrence of *H. ernsti* represent an intra-shelf swell setting (comp. Stevens 1988, Kaplan 1988, 1991). The ammonoid assemblage is referred to as a nostoceratid/collignoniceratid assemblage here, which is a morphospace equivalent of the allocrioceratid/collignonioceratid fauna of the middle Upper Turonian *Hyphantoceras* Event (comp. Fig. 3) of Kaplan & Kenndy (1996). At Salzgitter-Salder, the interval in question yielded only very few ammonites. So far, only two specimens of *H. ernsti* and *L. mantelli* were collected; fragments of scaphitids and baculitids occur but also in low quantities. The ammonite fauna may best be referred to as scaphitid/baculitid assemblage (Wilmsen & Wiese 2004, fig. 11), and it is rather the absence of any other morphologies that is indicative of the open shelf and off-swell settings.

The observed compositional difference between the ammonite assemblages of Groß-Flöthe and Salzgitter-Salder also finds its expression in the composition and quantity of the associated macrofauna. At Groß-Flöthe, hexactinellid sponges (a.o. *Cystispongia*, *Camerospongia*), echinoids (*Echinocorys*), large terebratulid brachiopods, pleurotomariid gastropods and remnants of giant inoceramids (see Wiese & Kröger 1998 for details) are not uncommon, while none of the elements listed above were collected at Salzgitter-Salder so far. Only thin-shelled inoceramids and *M. scupini* occur frequently. This rarity of ammonites and other macrofauna is not a sampling bias, as stratigraphic field exercises were carried out from the FU Berlin, FR Paläontologie in the last 4 years, during which the treated interval has been repeatedly and intensively collected over days. Triggering mechanism for the observed differences in diversity and abundance – implying a steady nutrient situation in the water body due to the remote open shelf position 200 km distant from any coastline – could result from increased water turbulence or current activity at or along swells,. The position of Groß-Flöthe as a submarine swell reflects increased disturbance resulting in an increased primary productivity in the sense of the intermediate disturbance hypothesis *sensu* Conell (1978) (see also Rosenberg 1995 and Sudgen et al. 2008).

5. Conclusion

The herein described faunule of *P. germari* doubles the scare record of the species from NW Germany. Although morphologically similar to the well-illustrated material from the Western Interior Seaway of the US, the presence of outer ventrolateral tubercles up to a size of ca. 55 mm indicates a regional population with individual characteristics. The main occurrence of the demersal species near intra-shelf swells correlates with the distribution pattern of collignoniceratids as observed elsewhere, which is explained by increased productivity and particle flux to the sea floor in the sense of the intermediate disturbance hypothesis. *Vice versa*, the situation in Salder rather reflects a system where current or turbulence induced disturbances are diminished, resulting in less productivity and particle flux to the sea floor. The observed limitation of the taxon to comparatively shallow settings in the upper part of the Salder Formation and its almost entire lack in remainder of the Upper Turonian (Grey and White alternation of the Erwitte Formation: major late Turonian sea level rise = latest Turonian peak of Hancock 1989) can, thus, be explained by ecological reasons.

6. Acknowledgments

M. Glos and M. Barlage (Berlin) are thanked for preparation and J. Evers for photographic works.V. Roden (Göttingen) smoothened the English. U. Kaplan (Gütersloh) is thanked for critical comments and discussion.

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Plate 1

***Prionocyclus germari* (Reuss, 1845) from the lower *Mytiloides scupini* Zone**
(all x 1)

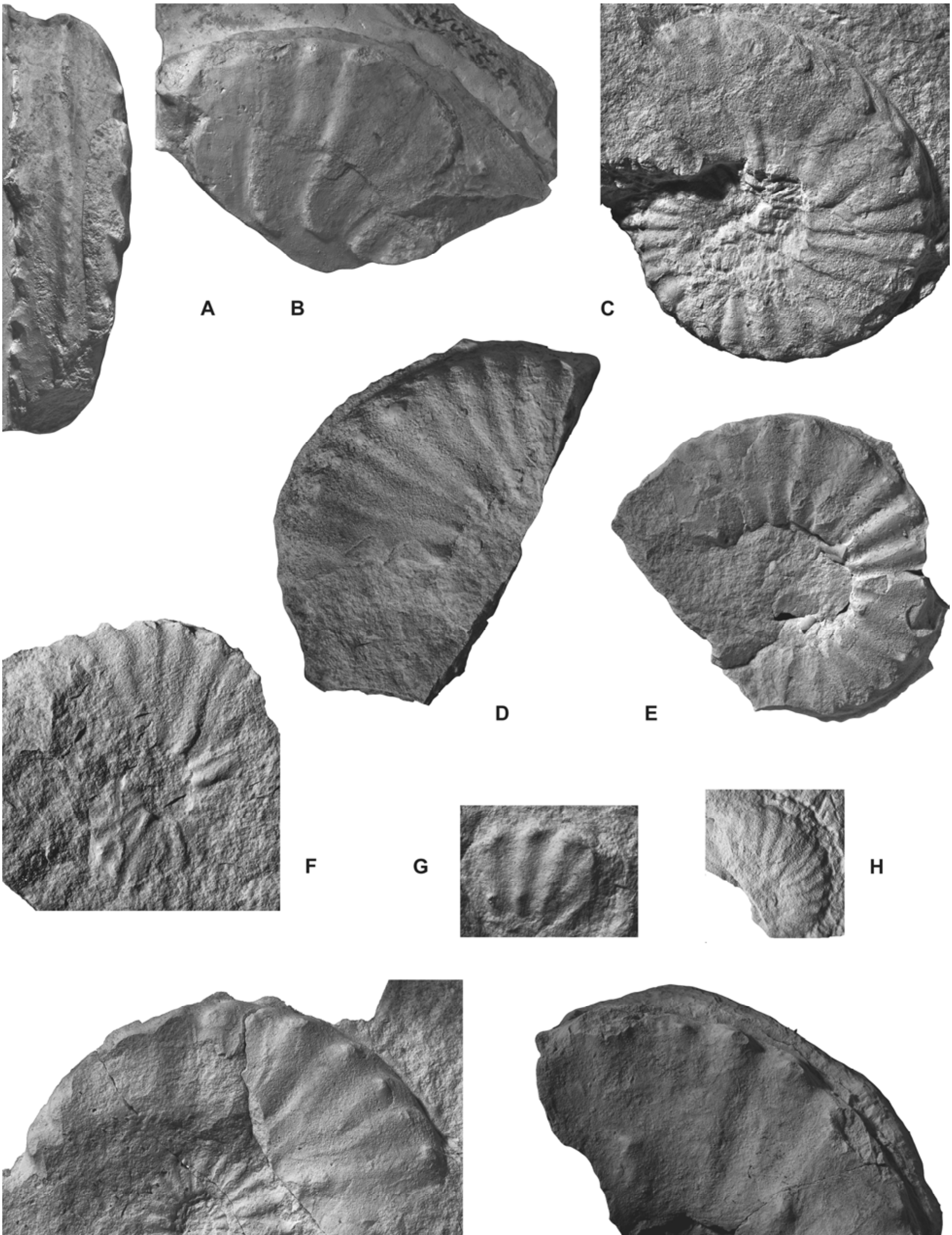
A, B: *Prionocyclus germari* (Reuss, 1845), Wüllen Formation of the Hollekamp Quarry, 5.80 m above Bed K6 of Ernst et al. (1998) (NwK 1).

C-E, H, I: *Prionocyclus germari* (Reuss, 1845) from the uppermost Salder Formation of Groß-Flöthe, loose from an interval between the *Micraster* Event below and the hardground above (see Fig. 4), (C: NsK 2, D: NsK 4, E: NsK 1, H: NsK 5, I: NsK3)

F: *Prionocyclus germari* (Reuss, 1845), uppermost Salder Formation, loose from an interval between the *Micraster* Event and the top of the Salder Formation, Dorstadt (NsK 6).

G: *Prionocyclus germari* (Reuss, 1845), uppermost Salder Formation, loose ca. 150 cm above the *Micraster* Event of Hoppenstedt (NsK 9).

J: *Prionocyclus germari* (Reuss, 1845), lower Erwitte Formation, Bed 17 of the Salzgitter-Salder quarry (comp. Fig. 4) (NsK 8).


A
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