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GEOLOGICAL SURVEY OF NAMIBIA



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MINISTRY OF MINES AND ENERGY



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Cover Image

**Panoramic view of Teufelskuppe : a carbonatite occurrence
in the Northern Sperrgebiet, Namibia, viewed from the southwest**

(Photo M. Pickford, 2018)

The Wanderfeld IV Cretaceous occurrence near Bogenfels, Namibia : the ammonite *Placenticer* and its associated bivalve fauna

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Abstract :- Careful preparation released an ammonite specimen from a block of highly indurated sandy limestone from the oyster bed of the Wanderfeld IV occurrence in Namibia. This find is important because Wanderfeld IV is one of two known marine onshore Cretaceous deposits on the west coast of Africa south of Angola. Although ammonites often permit precise dating of the beds in which they occur, the specimens from Wanderfeld IV are placenticeratids, most of which have low stratigraphic value because of the slow evolutionary changes that lineages in this family underwent and the provincialism that it shows. This is rather unusual among ammonites and thus, based solely on its ammonite record, the Wanderfeld IV site cannot be dated more precisely than probably Cenomanian to Coniacian.

However, the accompanying bivalve fauna consists of rare *Protocardia umkwelanensis* and abundant *Rhynchostreon suborbiculatum*, which gives its name to the oyster shell bed. Based on the bivalves, the Wanderfeld IV occurrence is likely to be Cenomanian. Rare microfossils from the same blocks of rock as the macrofossils did not yield precise stratigraphic information.

The Wanderfeld IV deposit is a bioclastic sandy limestone, representing a fully-marine, near-shore, high energy depositional environment as indicated by the presence of immature angular quartz grains in it. There are also a few well-rounded centimetric quartz pebbles in the limestone.

Key words :- Cretaceous, Ammonite, Bivalves, Biochronology, Depositional environment, Namibia

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Introduction

On a global scale, except for two regions, placenticeratid ammonites are generally rare in Late Albian to early Late Cretaceous ammonite faunas. Early *Placenticer* are unusually common in the Transcaspian region (NE Iran, Turkmenistan, SW Kazakhstan; Seyed-Emami *et al.* 1984; Kennedy *et al.* 2008). This is remarkable because in northern Europe, placenticeratids are scarce despite otherwise strong palaeobiogeographic relationships with the Transcaspian region. *Placenticer* is abundant in the Coniacian of South Africa, and this can be regarded as another exception to the general rule. The usually rare occurrence of the genus during its early evolutionary history explains why many species of *Placenticer* were based on limited material and are thus poorly

understood. Kennedy *et al.* (1981) and Kennedy & Juignet (1984) emphasized that placenticeratids were highly variable. During the past three decades, descriptions of the faunas from Kazakhstan and South Africa in particular, underlined the enormous variability in shell shape within each of the fossil populations and thus allowed critical revisions of a large number of previously described species (Klinger & Kennedy, 1989; Kennedy *et al.* 2008). Among the species that are difficult to interpret because they are based on only a few specimens, is *Placenticer merenskyi* that was described by Haughton (1930a) on the basis of a single specimen from near Bogenfels in Namibia (Figs 1, 2) but now represented by an additional specimen from the same area.

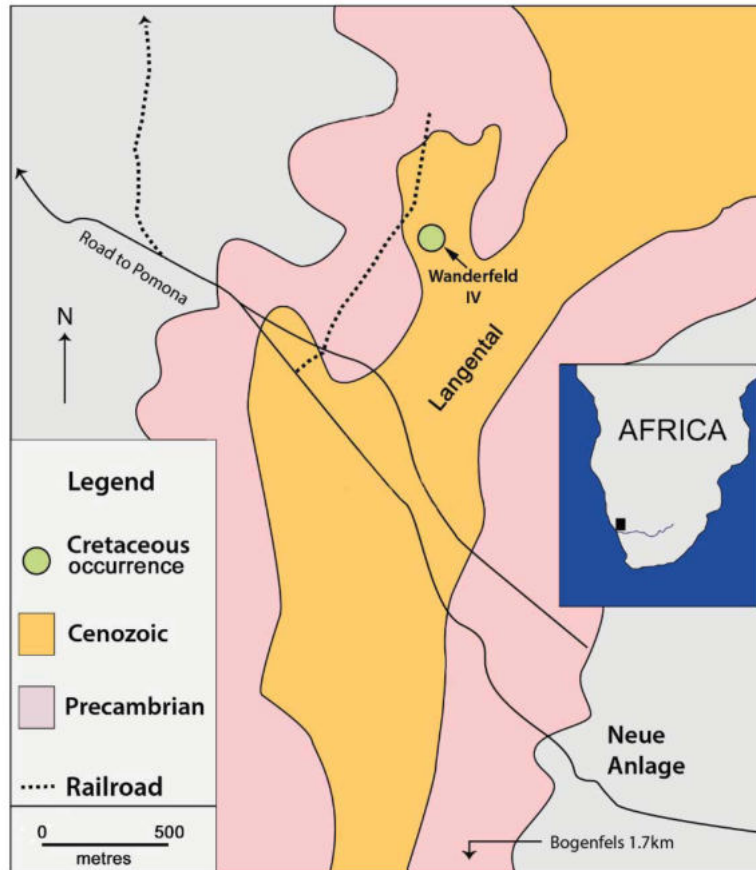


Figure 1. Location of the Wanderfeld IV Cretaceous occurrence in the Bogenfels area, southwestern Namibia (27°23'53.2"S ~ 15°24'19.8"E).



Figure 2. View from the north of the Cretaceous occurrence at Wanderfeld IV (surrounded by fence posts enclosing an area ca 20 x 20 metres in extent). During mining activities carried out from 1918-1920, the surface was partly obscured by numerous trommel-screen heaps.

The locality of Wanderfeld IV in the Sperrgebiet, Namibia, has yielded abundant oyster fossils, rare cardiid bivalves and four specimens of ammonites. The first ammonite discovered was the reasonably well-preserved holotype of *Placenticerus merenskyi* Haughton 1930b (Fig. 7). The second was a tiny fragment of an open-coiled heteromorph, possibly *Allocrioceras*, referred to by Klinger & McMillan (2007) as *Glyptoxoceras?* sp. A rock fragment collected by one of us (MP) in 2015 contained three placenticeratids, two fragments (see Fig. 4, right image) and a more complete specimen (Fig. 4, left image; Figs. 5 & 6). The small fragments were ground off in order to expose the best preserved ammonite from Wanderfeld IV that is the main subject of the present paper.

This is a significant find because it represents new material that can be compared with the enigmatic, unfortunately poorly preserved and, thus far, unique specimen of *Placenticerus merenskyi*. The new specimens were found 85 years after the first ammonite

was discovered at Bogenfels and shed new light on the taxonomic status of *Pl. merenskyi*.

The status of the species has been actively debated in the literature concerning Cretaceous ammonites, some authors doubting its status. This renders the new material particularly relevant. Two of the ammonite specimens in the block of limestone were fragmentary and were ground off before careful preparation of the most complete individual was undertaken. The latter is a phragmocone with an initial part of the body chamber, and its excellent preservation allows features to be observed more clearly than in the type specimen of *Pl. merenskyi*. Thus, comparison with other species described in the literature can be based on a more informative foundation.

Apart from its relevance to the taxonomy of ammonites from Namibia, the new discovery has implications for estimating the geological age and depositional environment of the Cretaceous deposits at Wanderfeld IV, which could throw light on the geological and geomorphological development of Namibia during this period.

Material and methods

The new ammonite specimen from Wanderfeld IV is curated at the Geological Survey of Namibia in Windhoek, Namibia, under the inventory number GSN F1635, whereas the cardiid bivalve is catalogued as GSN F1755.

The acronym SAM (South African Museum, now the Iziko South African Museum, Cape Town) is used with respect to the inventory number of the holotype of *Placenticerus merenskyi*.

Some of the figured specimens were coated with ammonium chloride to highlight morphological details. According to a recent review of photographic methods by Krogmann & Lehmann (2016) this is an informative way of highlighting morphological features in fossils

Scanning electron microscope (SEM) images of rock samples extracted from the

matrix of the ammonite were taken at the Faculty of Geosciences Bremen, with a Zeiss Supra 40. Elemental composition was investigated via a Bruker EDX X-Flash 6130 analyzer. The software used for elemental analysis was Bruker Qantax-Espirit 1.9. The x-axis (keV) shows the energy emitted when electrons change their electron shell, the y-axis (cps/ev) indicates the presence of the element in that particular energy level that arises from dislocation of the electrons, measured in counts per second. All samples were sputtered with gold following standard procedures and thus several Au peaks can be seen in the spectra. Measurements in Atom % are given for each spectrum (see results). All measurements refer to the K-Series.

Sample preparation

The ammonite specimen from Wanderfeld IV was found embedded in a strongly indurated sandy limestone (Figs 4, 5A-5B). Estimations of the composition of the rock in % were made based on the charts of Flügel (2010). Before careful preparation of the

specimen at Bremen, the left side of the specimen was cleaned to some extent with traditional tools (Step A1 in Fig. 5). The contact between the fossil and the surrounding rock is poorly defined and we thus employed a combination of preparation methods using

pneumatic chisels and air abrasion. Chiseling was done mainly with a HW70 and abrasion by a HW120 using 70 μm iron powder (both devices manufactured by Hardy Winkler, Schiesheim, Germany). The entire preparation was performed under a binocular microscope (LEICA Wild M715). In the case of the calcareous shells from the Wanderfeld IV site (Fig. 3B), the contact between the fossil and the sediment is discontinuous as can be seen in the SEM images (Figs 3A and 3C).

Figure 5B shows the state of the specimen after removal of a thick layer of matrix from the right side of the specimen using an angle grinder and a coarse pneumatic chisel, while step Fig. 5A3 illustrates that a few millimetres of matrix (m) was still left on the surface of the shell (s) of the last tip of the body chamber preserved at this stage. Figure 5B shows the ongoing preparation process after the step in Figure 5A1, alternating between fine pneumatic chisels and air abrasive methods, while the red arrows indicate the positions of the umbilical tubercles to ensure their preservation. In the matrix on the left side of step 5B, some whitish shell fragments can be observed. Figures 5C and 5D represent subsequent stages in the preparation showing that the matrix contains scattered mineral aggregates with a maximum length greater than 1 mm. These

steps also show that this mineral is particularly concentrated in some areas near the surface of the fossil, passing into the ammonite shell itself. This is clearly visible in the colour image of the specimen (Fig. 5E). This mineral is pyrolusite (manganese oxide; see the EDX-analysis and its interpretation below). As a consequence, locally there is not a well-defined surface separating the fossil from the rock, which results in a partly perforated shell since the abrasion method employed to clean the fossil penetrated into the softer, blackish calcite (clearly visible in the coated specimen, see Fig. 6). To minimise damage to the fossil, the nozzle of the HW120 hand-held abrasive device was angled almost parallel to the surface of the ammonite shell and the final step is represented by Figure 5A-5C.

The matrix around most of the macrofossils from Wanderfeld IV was recovered during mechanical preparation and was studied for micropalaeontological purposes. Because the embedding limestone is highly indurated, thin sections were made. Microfossil extractions were also attempted using acetolysis dissociation techniques and the thermal shock (freeze-thaw) method, but without success. The disaggregated sediments were washed on sieves with successive mesh sizes of 63 μm and then dried at 90 $^{\circ}\text{C}$.

Figure 3. SEM images, EDX spectra and thin sections of the oyster shell bed containing *Placenticeras merenskyi*. A) Overview of a rock fragment of the ammonite matrix, showing a fracture that has been filled secondarily by calcite and a calcitic shell fragment, presumably of an oyster. B) EDX spectrum of one of the large crystals filling the rock fracture depicted in 'A'. C) Shell fragment, presumably an oyster shell, recrystallized and structurally hardly distinguishable from the limestone matrix; green: nacreous layer, blue: prismatic layer. D) EDX spectrum of the centre of the prismatic shell layer in 'C'. E) Vaguely delimited lighter stains in this SEM image correspond to the blackish mineral aggregates that are macroscopically visible in the matrix. These turned out to be manganese oxide by EDX evidence. F) EDX spectrum of the vaguely limited lighter stains interpreted as manganese oxide and depicted in 'E'. G) Quartz crystals that underwent elemental analyses are coloured reddish. H) EDX spectrum of the upper grain of the supposed quartz crystals that is coloured reddish in 'G'. I) Thin section showing small globular planktonic foraminifera with a Muricohedbergellid-type morphology. J) Planktonic foraminiferan with thick test composed of ridges, apparently a reticulate system (honeycomb pattern).

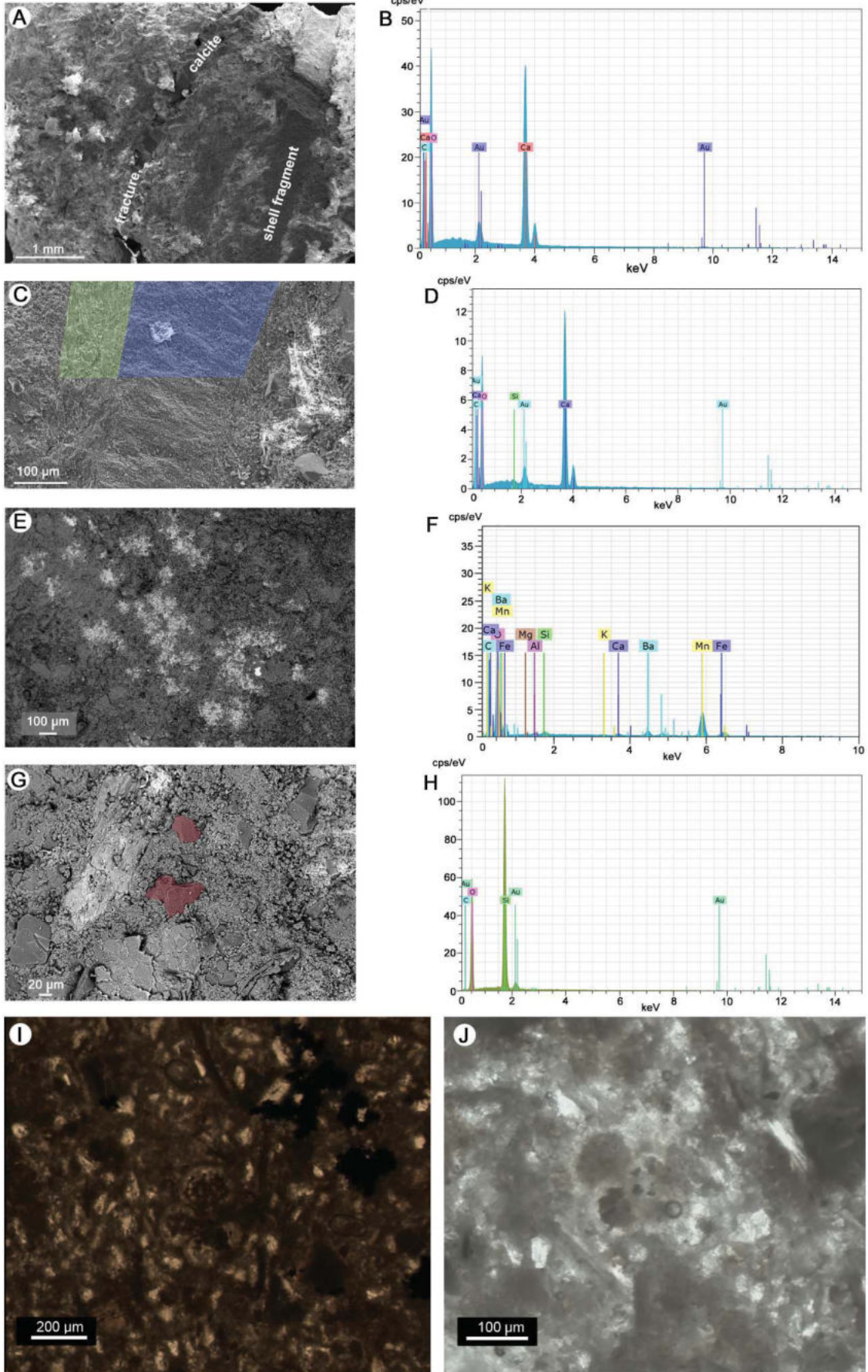


Figure 3. Legend on page 35



Figure 4. Three shells of *Placenticerus merenskyi* in a block of calcareous sand collected from Wanderfeld IV in 2015 (GSN F1635) prior to removal of the matrix.

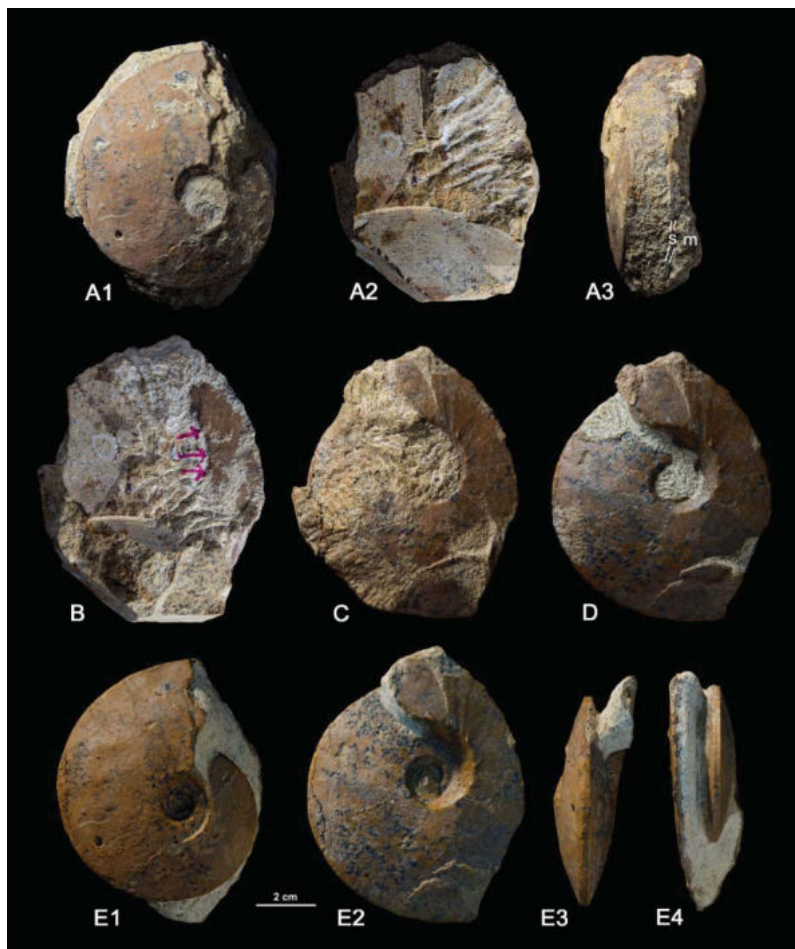


Figure 5. Preparation stages of specimen GSN F1635. A) the raw specimen after cutting a large portion of matrix off the right side of the ammonite and initial chiseling (A2), the most apertural part was weathered out and was visible in cross section (“s” in A3; with matrix to the right indicated by “m”), B) shows ongoing preparation with pneumatic chisels, with arrows pointing to the delicate umbilical tubercles to save them from damage during work in progress, C) the surface after blasting with fine iron powder, D) after additional alternating chiseling and blasting, E) the final stage of preparation, clearly showing blackish stains of manganese oxide covering and penetrating the shell.

Systematic Palaeontology

Ammonites

Superfamily Hoplitoidea H. Douvillé, 1890

Family Placenticeratidae Hyatt, 1900

[= Hypengonoceratinae Chiplonkar & Ghare, 1976, p. 2; Baghiceratinae Chiplonkar & Ghare, 1976]

Remarks

Kennedy & Wright (1983) recently provided diagnoses of the genera of Placenticeratidae and outlined the difficulties

encountered in attempts to subdivide the mainstream stock of the family.

Genus *Placenticeras* Meek, 1876

Type species :- *Ammonites placenta* DeKay, 1828, p. 278, by original designation of Meek (1876, p. 46).

Species *Placenticeras merenskyi* Haughton, 1930a

Holotype :- By monotypy, SAM-10569 from the Cretaceous of Bogenfels, Namibia (Haughton, 1930b, p. 363, pl. 11, figs 1-3; refigured by Klinger 1977, fig. 7; Klinger & Kennedy, 1989, figs 99-100, including ventral and dorsal views; refigured here as Fig. 7).

Material :- GSN F1635 from the Wanderfeld IV oyster shell bed (Figs 4-6). A 3D model in wavefront OBJ format with texture as JPG is stored at PANGAEA® Data Publisher (<https://www.pangaea.de/>). This model was prepared by Martin Krogmann (Geowissenschaftliche Sammlung, Universität Bremen) and can be viewed with all current 3D viewers

(e.g. MeshLab) and can be accessed via DOI: <https://doi.org/10.1594/PANGAEA.946500>.

Synonymy :-

- 1930a *Placenticeras merenskyi* sp. nov.; Haughton, p. 363; pl. 11, figs. 1-3
- 1977 *Proplacenticeras merenskyi* (Haughton); Klinger, fig. 7
- pars* 1989 *Placenticeras kaffrarium* Etheridge, 1904; Klinger & Kennedy, p. 268, figs 9-14A, 19-20, 22-99
- 2015 *Placenticeras merenskyi*; Pickford & Senut, p. 6, left figure

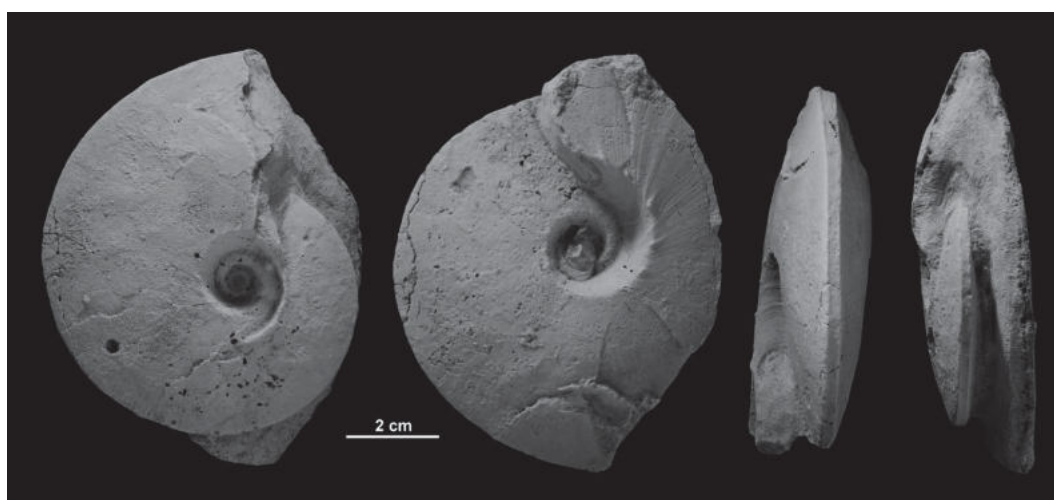


Figure 6. *Placenticeras merenskyi*, GSN F1635, images of coated specimen highlighting morphological details.

Description

This three-dimensionally preserved phragmocone with part of the body chamber has a maximum preserved diameter of 82.4 mm and a reconstructed diameter of about 110 mm. There is almost no distortion at the phragmocone-body-chamber transition and in the area closest to the aperture. The shell is preserved but, particularly on its right side, the suture lines are rudimentary but can be discerned. The coiling is very involute, about 14 per cent of the total diameter. In cross section the whorls are compressed (Fig. 8A). They reach the greatest whorl breadth at the umbilical edge and taper to a narrow, flattened to slightly sulcate, venter. The length of the body chamber

is equivalent to at least half a whorl. At first sight the shell appears to be completely smooth. However there are a strongly prorate, fine growth striae and a few faint falcoid swellings on the flanks preserved on the last quarter whorl. There are fine elongated umbilical tubercles or bullae, about 8 per half whorl. Tuberculation is probably not developed before the body chamber (this feature is obscure on the phragmocone). The umbilical wall is well rounded on the innermost whorls with a well-developed umbilical edge, while on the body chamber, the wall stands at an angle of 45 degrees to the median plane of the shell.

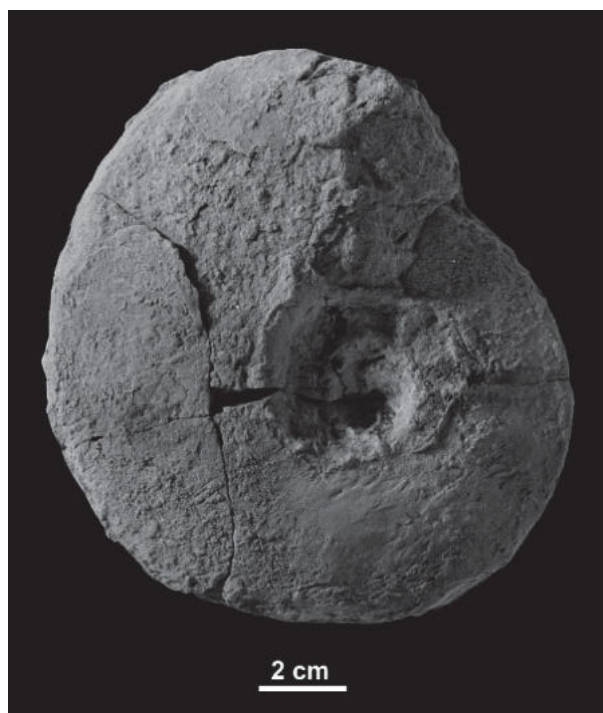


Figure 7. Lateral view of the type specimen of *Placenticerus merenskyi*, SAM-10569, original of Haughton, 1930b, pl. 11, figs 1-3; this image was also figured by Klinger (1977, fig. 7) and Klinger & Kennedy (1989: fig. 99).

Comparison with the holotype

Comparison between the morphological features of GSN F1635 and those of the type specimen (SAM-10569, Fig. 7) needs to take into account the different sizes of the specimens (Fig. 8). The holotype of *Placenticerus merenskyi* has a maximum preserved diameter of 125 mm in contrast to the maximum preserved diameter of 85 mm in the new material and both are phragmocones with a part of the body chamber preserved. Despite

these differences, it is clear on first sight that the cross section at corresponding diameters, that GSN F1635 is smaller than SAM-10569 (Fig. 8). Especially the portion of the flattened venter is much smaller in GSN F1635 compared to a similar diameter (around 85 mm) in the type specimen. The earlier whorls of SAM-10569 also show a sulcate venter for at least one whorl (see Haughton, 1930b: fig. 2) whereas it is flat at all visible growth stages in GSN F1635. In

addition to these features, a fold-like ribbing of very shallow ribs is present, at least on the late phragmocone of the type specimen (at 40-50 mm whorl height; Haughton 1930b, p. 363, points out that “*the external features of the lateral surface are not well displayed*”). In contrast, there are a few barely discernible, shallow folds visible in GSN F1635 (visible at a whorl height of 30-40 mm, best preserved on the left side of the shell). Haughton (1930b)

emphasized the main ornamentation of very small umbilical tubercles, twelve on the last whorl. In GSN F1635 these are clearly visible on the last half of the ultimate portion preserved on the right side of the specimen. Extrapolated to one whorl their number in GSN F1635 was probably slightly lower, but an exact comparison is impossible due to the smaller diameter of GSN F1635.

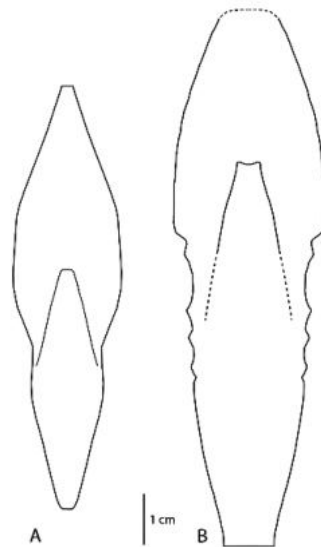


Figure 8. Diagrammatic cross sections of GSN F1635 (A) and of SAM-10569 (B) the type specimen of *Placenticerus merenskyi* (sketch of type specimen modified from Haughton 1930b: pl. XI, fig. 2).

Discussion

Klinger & Kennedy (1989) and Kennedy *et al.* (2008) showed that study of the ontogenetic development of *Placenticerus* is essential for understanding the morphological variation within the genus and thus its species taxonomy. Klinger & Kennedy (1989) differentiated between individual growth stages in *Pl. kaffrarium* from the Coniacian of South Africa, an exceptionally well-known species. Herein we number the stages 1 to 4:-

Stage 1) embryonic stage

Stage 2) early phragmocone stage =

umkwelanense stage:

- very compressed
- maximum breadth at umbilical shoulder
- smooth, except for fine falcoid or sickle-shaped striae
- curve of sickle-like ribs may be slightly greater than that of the

‘handle’, producing slight crescents on ventral half of the flanks
 venter concave to flat and smooth, bordered by entire, sharp, narrow ventro-lateral shoulders

Stage 3) middle to early-late phragmocone stage = *subkaffrarium* stage

- whorl section becomes more inflated and rounded
- umbilical shoulder becomes rounded
- umbilical tubercles of varying strength, about 7-8 per whorl, connected by single or bifurcating ribs of varying strength to weak or prominent lateral tubercles
- venter becomes tuberculate, with distinct alternating ventral clavi: centre becomes crenulate

Stage 4) late phragmocone and body chamber = *kaffrarium* stage

- whorl section becomes even more inflated and rounded

- umbilical tubercles migrate outwards and weaken
- venter becomes distinctly rounded and eventually smooth
- Lateral ornament may also weaken considerably towards and on the body chamber
- Umbilical seam may show slight egression on the body chamber: scaphitoid uncoiling

These four ontogenetic stages can be of different duration in individuals or may be omitted and thus comparisons between specimens of *Pl. kaffrarium* might be extremely difficult (Klinger & Kennedy, 1989). A similar succession of ontogenetic stages can be observed in a large collection of *Placenticerias kolbajense* from the Late Albian of Magyshlak in Kazakhstan (Kennedy *et al.* 2008) suggesting that the observation first made on the basis of Coniacian material from South Africa can possibly be generalized to the genus as a whole.

Based on the two specimens from Namibia this subdivision is comprehensible. The largest portion of GSN F1635, with its very compressed coiling, maximum breadth at umbilical shoulder and sharp, narrow ventro-lateral shoulders represents stage 2; the fragmentary portion of a last quarter of a whorl preserved on the right side of the specimen might be assigned to an initial part of ontogenetic stage 3, with its cross section that is increasing rapidly, and umbilical tubercles that give rise to single or bifurcating ribs of varying strength. The type specimen, which is distinctly larger than GSN F1635, is poorly preserved with no indication of ribbing, and whether or not the umbilical shoulder becomes rounded is difficult to say (see above and Klinger & Kennedy 1989: p. 350). Nevertheless, it agrees well with stage 3 in having umbilical tubercles and a whorl section that becomes more inflated and rounded. The type specimen does not develop lateral tubercles as in *Pl. kaffrarium* during stage 3, but this feature is also missing in that stage in *Pl. kolbajense* (Kennedy *et al.* 2008).

Based on the knowledge about these ontogenetic stages, including the individual timing and the potential skipping of such stages, plus the fact that the intraspecific variability in *Placenticerias* can be high, it is likely that, despite their different morphologies, the two

specimens from Wanderfeld IV belong to the same species.

Being confident that SAM-10569 and GSN F1635 are conspecific, the question is now to determine whether *Placenticerias merenskyi* should be regarded as a distinct species based upon the features and variability established for the Namibian material, or not.

Placenticerias merenskyi was questionably synonymised by Howarth (1985; a synonym of *Placenticerias kaffrarium*, see Klinger & Kennedy, 1989) with his *Proplacenticerias stantoni* var. *bolli* and later by Klinger & Kennedy (1989) with *Placenticerias kaffrarium*. Cooper (1995: p. 37) indirectly suggested synonymy between *Placenticerias merenskyi* and *Placenticerias memoria-schloenbachi* (Laube & Bruder, 1887) by identifying the Wanderfeld IV ammonite as *Pl. memoria-schloenbachi* and subsequently (Cooper, 2003: p. 120) he stated that, in his opinion, *Pl. merenskyi* represents a junior subjective synonym of it, by emphasising the small and more numerous umbilical tubercles as a diagnostic feature. *Pl. memoria-schloenbachi* from the Bohemian lower Turonian, however, is poorly known, and we agree with Klinger & Kennedy (1989: p. 350) that interpretation of this species is problematic. The original figure is schematic with 10 elongated umbilical tubercles per whorl (Laube & Bruder, 1887: p. 221 state a number of 11) “and a narrow venter with sharp shoulders and no ventral clavi to a great diameter” (Klinger & Kennedy, 1989). Wanderer (1909) reported specimens from Saxony, Germany, and thus from a region close to the area where the type material was collected, but from Cenomanian strata, in which the umbilical bullae are worn and the ribs are indistinct and shallow. Other material from the Lower Turonian and Upper Cenomanian of Saxony, questionably referred to this species, does not show tubercles or any ornamentation (Wilmsen & Nagm, 2013, 2014). However, the few available specimens are distorted and are generally poorly preserved and are thus not fully diagnostic (Wilmsen & Nagm, 2013, 2014). In fact, not one of the more recent authors referred their material to *Pl. memoria-schloenbachi* without doubt (see synonymy in Wilmsen & Nagm, 2013). This is why we do not follow Cooper (1995) and Cooper (2003) in synonymising *Placenticerias merenskyi* with *Pl. memoria-schloenbachi*.

We agree with Klinger & Kennedy (1989, p. 349) that *Placenticerias merenskyi* is

“a difficult species to interpret”. The new specimen from Wanderfeld IV is, however, much better preserved than SAM-10569 and suggests that the placenticeratids from the Wanderfeld IV Cretaceous occurrence are no exception to the general observation about the group being highly variable as demonstrated by other *Placenticerases* samples from localities in Asia and Africa. Klinger & Kennedy (1989) assumed that, since oyster epizoans and surplus matrix is hindering their assessment (Fig. 7), the umbilicus in *Pl. kaffrarium* is wider than usual and that the number of umbilical tubercles is higher than on average in *Pl. kaffrarium* (12 in contrast to 7-8). Although SAM-10569 does not show a tuberculate venter, Klinger & Kennedy (1989) used this feature to postulate similarities to *Proplacenticerases memoriaschloenbachi* var. *ambiloensis* Collignon (1965) and thus to their type 2 or 4 of *Pl. kaffrarium*, because this ventral feature is normally associated with umbilical tubercles and these are present in *Pl. merenskyi*. In this feature GSN F1635 agrees with the type specimen of *Pl. merenskyi* and thus confirms that *Pl. merenskyi* represents a distinct species.

The non-tuberculated venter of *Pl. merenskyi* also serves to reject synonymy with *Proplacenticerases stantoni* var. *bolli* (Hyatt, 1903) from the Cenomanian of Texas, discussed by Howarth (1985, p. 85). The latter taxon is based on fairly rich material that shows considerable variability. Howarth (1985) claimed that the holotype of *Placenticerases merenskyi* established “by Haughton (1930: 363; pl. 11, figs. 1-3) is very close in all visible features to the inner whorls of the Texas specimens, and the specific name is probably a synonym”. Except for the very mature smooth body chamber figured by Hyatt (1903, pl. 42) all of his specimens show extremely well-developed ventro-lateral clavi and thus it appears unlikely that the Namibian and Texan samples are conspecific.

Morphologically similar are the Caspian species *Pl. kolbajense* (Sokolov, 1967) from the Upper Albian and *Pl. mediasiaticum* Luppov, 1963, from the Lower Cenomanian (Kennedy *et al.* 2008). In contrast to *Pl. merenskyi*, *Pl. kolbajense* bears ventro-lateral tubercles when showing umbilical bullae. Furthermore, the umbilical bullae are far more distant in *Pl. kolbajense*. Apparently *Pl. mediasiaticum* is a highly variable species, but it usually shows a broader cross section during mid-growth, a ribbing that is not restricted to flattened folds on the outer flank and at this stage a crenulated venter is established prior to the appearance of the ventral clavi – all of which are lacking in *Pl. merenskyi*. Whether *Pl. grossouvrei* Luppov, 1963, also known from the Caspian area, can be regarded as a separate species or not, it is noted that it differs from *Pl. merenskyi* by its stronger ribbing and stronger umbilical bullae (Seyed-Emami *et al.* 1984). *Pl. gaurdakense* Luppov, 1963, is also much more robustly ornamented than *Pl. merenskyi*, with a broader cross section.

As was pointed out in the introduction, placenticeratids are known to be highly variable (Kennedy *et al.* 1981; Kennedy & Juignet, 1984; Klinger & Kennedy, 1989; Kennedy *et al.* 2008) as shown by the morphological variation in comprehensive samples from Kazakhstan and South Africa. Recognising that *Pl. merenskyi* also appears to display high variability means that a detailed comparison with *Pl. kaffrarium* would be satisfactory only if there were more than two specimens of *Pl. merenskyi* available from the Wanderfeld IV occurrence, but such is not the case.

In summary, the affinities of *Pl. merenskyi* remain somewhat obscure, but GSN F1635 appears to confirm that *Pl. merenskyi* represents a distinct species. As interpreted here, as in other species of *Placenticerases*, *Pl. merenskyi* is likely to have been highly variable in morphology.

Bivalves

The Wanderfeld IV Cretaceous occurrence contains abundant fossil shells of oysters, for which reason these beds were called the *Exogyra* beds by Haughton (1930a, b) or the *Rhynchostreon* shell bed by Klinger (1977). These oyster fossils were figured by Klinger (1977, here depicted in Fig. 9). The Namibian

occurrence has been mentioned in the literature several times (Cooper, 1995, 2003). We do not present any new morphological data about these fossils but, in the discussion section, we focus on the stratigraphic value of the species concerned, which is identified as *Rhynchostreon suborbiculatum*.

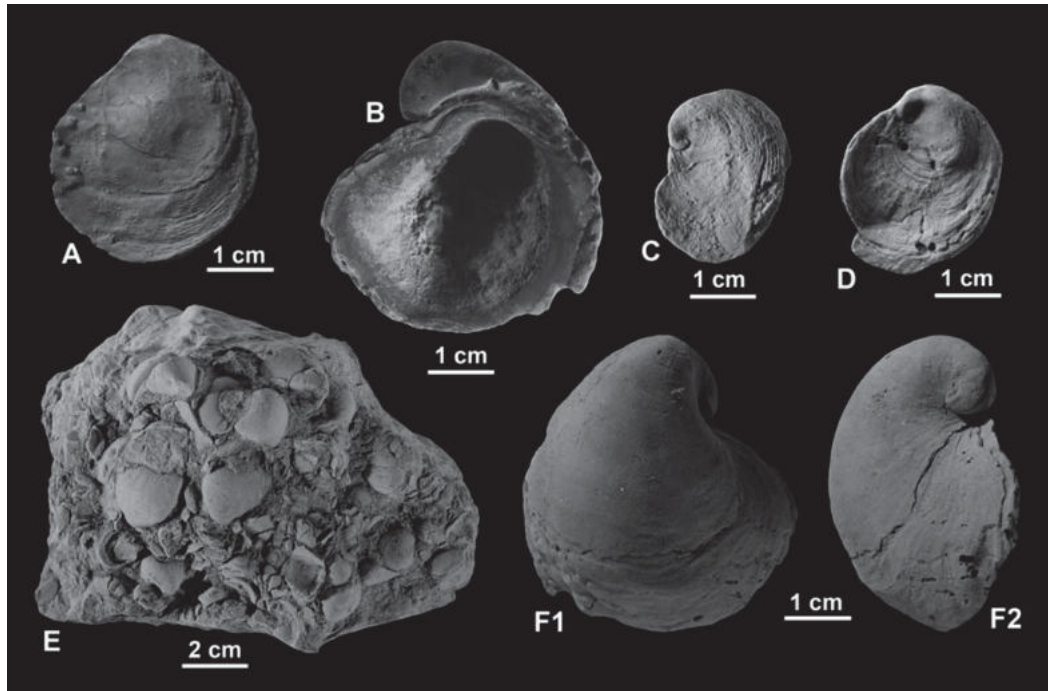


Figure 9. *Rhynchostreon suborbiculatum* (Lamarck, 1809) Late Cretaceous, Wanderfeld IV, near Bogenfels, Namibia. A-C: right single valves (A, C) and left single valve (B). D: right single valve, scan of a negative photo of Klinger (1977: fig. 8G). E: rock specimen with an accumulation of *R. suborbiculatum*, scan of a negative photo of Klinger (1977: fig. 4). F: left single valve. A-C and F from negative photos by Herbert Christian Klinger, but not depicted by Klinger (1977).

Order Veneroida H. Adams & A. Adams, 1856

Superfamily Cardiaceae Lamarck, 1809

Family Cardiidae Lamarck, 1809

Subfamily Protocardiinae Keen, 1951

Genus *Protocardia* Beyrich, 1845

Species *Protocardia umkwelanensis* Etheridge, 1904

Material :- GSN F 1755 right valve (Figs 10 and 11).

Synonymy :-

1904 *Protocardium hillanum*, J. Sowerby., sp.,
var. *umkwelanensis*, var. nov.;
Etheridge, p. 79; pl. 1, fig. 6
1906 *Protocardia Hillana* (Sowerby) var.;
Woods, p. 307; pl. 37, fig. 6

1969 *Protocardia hillana*; Haughton, pl. 50.5
2018 *Protocardia umkwelanensis* Etheridge;
Cooper, pl. 44D (drawing, based on
Woods, 1906)

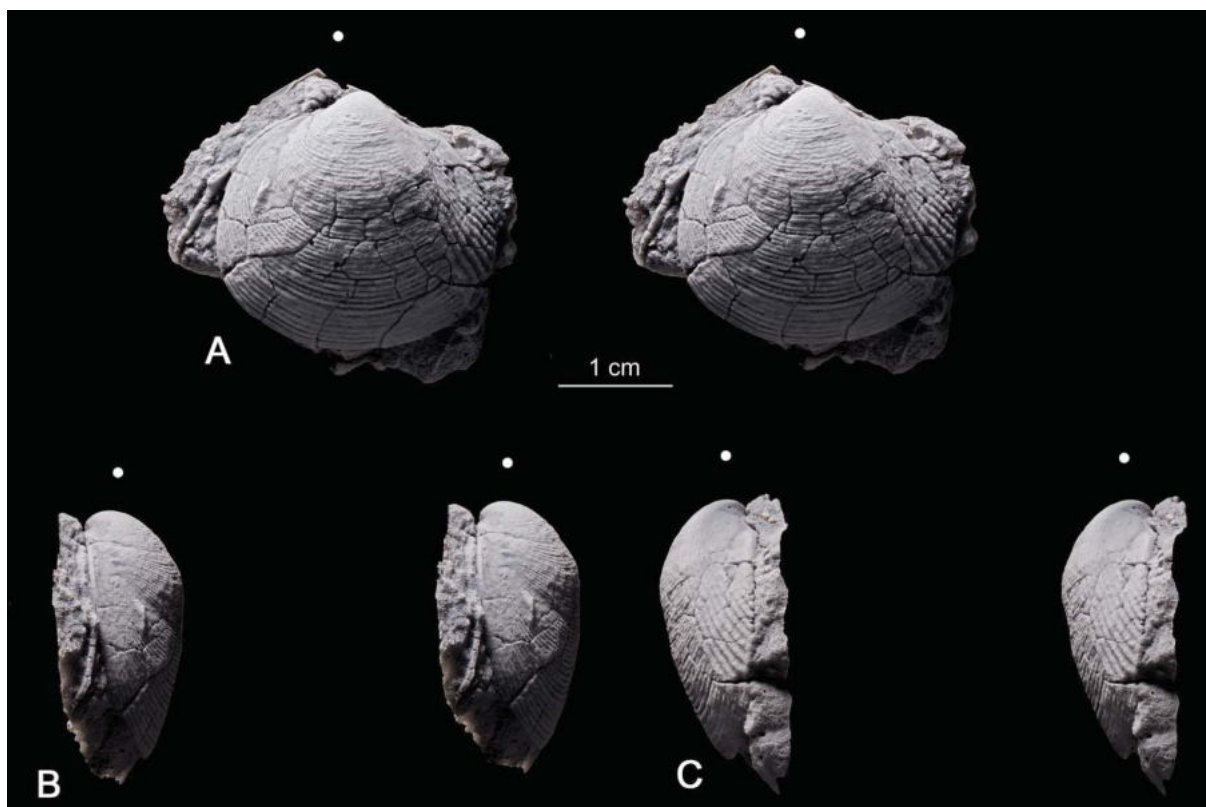


Figure 10. Stereo images of **GSN F1755**, right valve of *Protocardia umkwelanensis* Etheridge, 1904, from the Wanderfeld IV Cretaceous occurrence near Bogenfels. A) superior view, B) anterior view C) posterior view.

Description

GSN F1755 consists of a small, isolated right valve with a maximum shell length of 25.5 mm and a maximum shell height of 23.5 mm and is thus slightly higher than broad (Fig. 10). The outline of the valve is sub-round, with a medially positioned umbo that is almost pointed, narrowly rounded and passing into a strongly convex antero-dorsal margin that

continues gradually into a strongly convex ventral margin. Numerous concentric, fine but prominent and regular ribs cover most of the shell. At the posterior rim, that is fairly truncated, 10 radial flank ribs are counted instead of concentric ribbing; the radial ribs are clearly more prominent and have broader interspaces compared to the concentric ribs.

Discussion

Etheridge (1904) described *Pr. umkwelanensis* as a variety of the type species of the genus, *Protocardium hillanum* Sowerby, 1813, from the early Coniacian of KwaZulu-Natal (South Africa) where it is common (pers. comm. Michael Cooper, April 24, 2022; Fig. 11). The specimen figured by Woods (1906) from the same country, refigured by Cooper (2018) is from the Santonian part of the Mzamba Formation (= Umzamba Formation,

see also Klinger & Kennedy, 1980; Ovechkina *et al.* 2009) and the species appears to be absent from the Campanian part of this formation (Cooper & Greyling, 1996). Due to the regional latest Cenomanian-Turonian unconformity, the first occurrence of *Pr. umkwelanensis* in KwaZulu-Natal is not recorded, but Cooper (2003: p. 91) recorded it from the uppermost Cenomanian, Turonian or early Coniacian of Angola.

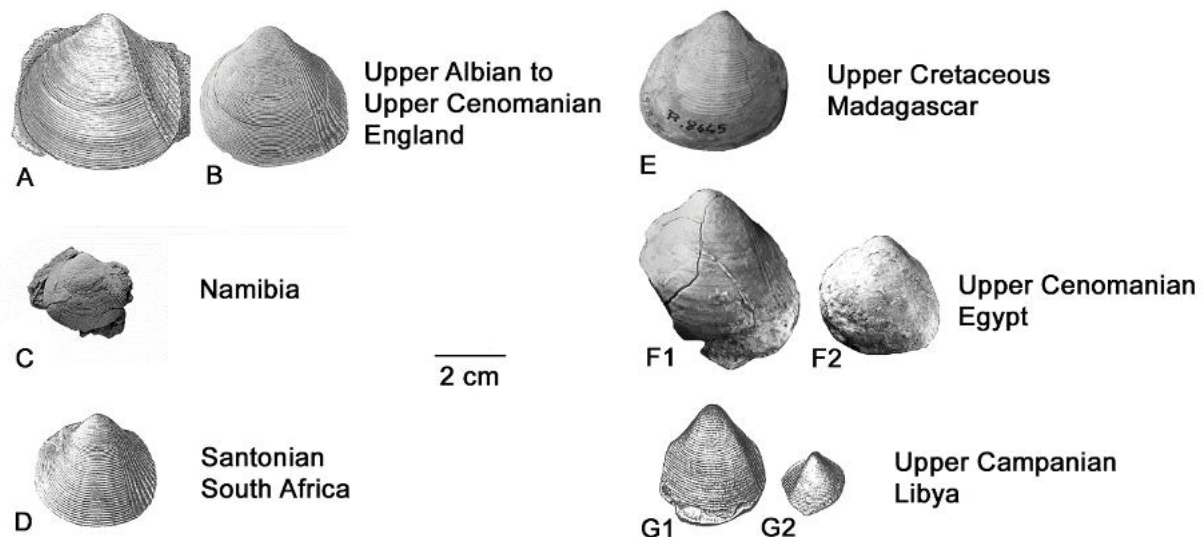


Figure 11. *Protocardia umkwelanensis* Etheridge, 1904, from Namibia (GSN F1755) compared to the closely allied *Protocardia hillana* (J. Sowerby, 1813) originally described from England, and other African material assigned to the genus *Protocardia*. A) Original figure of *Pr. hillana* Sowerby from Sowerby (1813, mirror image of his pl. 14: upper figure) and B) *Pr. hillana* of Woods (1908; fig. 2 = his pl. 12, fig. 1) from the Upper Albian/Lower Cenomanian of England. C) *Pr. umkwelanensis* from the Wanderfeld IV Cretaceous occurrence near Bogenfels, GSN F1755. D) *Pr. umkwelanensis*, original figure of Woods (1906) from the Santonian Mzamba Formation of South Africa, E) *Protocardia* from the Late Cretaceous of Madagascar and referred to *Pr. hillana* by Basse (1932) taken from <https://www.gbif.org/occurrence/418904320> (creative commons license). F1, F2) *Protocardia* from the Upper Cenomanian Raha Formation of Egypt, and referred to *Pr. hillana* by El Qot (2006: pl. 16, figs. 4-6), G1, G2) *Protocardia* from the Upper Campanian of Libya, referred to as *Pr. hillana* by Quaas (1902: pl. 24, figs. 18-19).

Morphologically *Pr. umkwelanensis* and *Pr. hillanum* show great similarities to each other as was already indicated by the early workers (Fig. 11). Whereas the former species is not recorded prior to the Upper Cenomanian, the latter one occurs in the type area in southern England in the late Albian and early Cenomanian, but is believed to range up into the Maastrichtian (El Qot, 2006). However, we infer that *Pr. hillanum* is used as a waste-basket taxon, the divergent morphologies of other African specimens described in the literature appearing to confirm this view (Fig. 11). In fact, Merensky (1909: p. 18) already referred to a bivalve from the Sperrgebiet as *Pr. hillanum*

(cf. Haughton, 1930a: p. 361). We follow Cooper (2003, 2018) in separating the two species and have some good arguments for doing so. The concentric ribbing appears to be more prominent in *Pr. umkwelanensis* and the outline is more sub-rounded and more symmetrical with reference to the medial line, and possibly the maximum length of *Pr. umkwelanensis* is less. Another argument is that a form assignable to *Protocardia hillana* is present in the latest Albian *cristatum* Zone in Zululand, but it appears to be missing from the Lower Cenomanian (pers. comm. Michael Cooper, April 23, 2022).

Matrix of the ammonite block

In the following section, the limestone in which the Wanderfeld IV ammonite was found is analyzed by SEM images and EDX elemental analysis (EDX, Fig. 3 and Table 1). As already described in the “Materials and Methods” section, the sedimentary rock is spotted with blackish mineral aggregates that significantly hindered preparation of the ammonite specimen. For this reason, an EDX was performed, which revealed that the spots

consist of pyrolusite (manganese oxide) (see Fig. 3F) which appear as lighter stains in the SEM images (Fig. 3E). The manganese oxide is finely dispersed in the sediment (1% and more) but in some areas it is concentrated up to 40% (e.g. Fig. 3E) and seems to occur preferentially at the matrix-shell contact. Sporadically, small amounts of aluminium silicate are associated with the manganese oxide. The bioclastic limestone also contains grains of SiO₂ (Figs 3G

and 3H) and muscovite. The quartz grains (about 5 % estimated percentage) are immature and have average maximum dimensions of 50

to 100 µm. Occasional fractures can be seen in the limestone that have been filled with calcite (Fig. 3A).

Table 1. Selected EDX measurements of the matrix of GSN F1635 in Atom %. All measurements refer to the K-Series.

Element	Shell material	Filling of rock fracture	Manganese oxide	Quartz crystals
	Atom %	Atom %	Atom %	Atom %
C	17.91	18.64	--	5.56
O	65.19	67.87	70.4	64.80
Si	0.08	--	0.89	29.63
Ca	16.82	13.49	0.87	--
Mn	--	--	22.02	--
Mg	--	--	0.57	--
Al	--	--	0.66	--
K	--	--	0.26	--
Fe	--	--	2.15	--
Ba	--	--	2.18	--

The rock matrix frequently contains shell fragments that are completely recrystallised. Figure 3B shows the structures typical of prismatic layers (broad layer, coloured bluish) and a nacreous layer (narrow layer, coloured greenish). The SEM image

illustrates the close bond between the fossil and the enclosing sediment, which rendered the extraction of the specimen so delicate. The EDX analysis unequivocally indicates calcium carbonate for the prismatic layer without any other significant elements.

Thin sections and Micropalaeontology

Thin sections of the Wanderfeld IV limestone blocks reveal the scarce presence of poorly preserved planktonic foraminifera. There are mostly small globular forms (Fig. 3I). One specimen (Fig. 3J) presents a thick test with an apparently reticulate system composed of ridges (honeycomb pattern). As these structures seem to be regular, they do not appear to be linked to diagenetic alteration. During the Cretaceous, only a few rare species present such structures. Dealing with the foraminiferan morphology and with the structure of the test, this form could be assigned to *Favusella washitensis*, which ranges in age from the Aptian to the middle part of the Cenomanian. However, this identification must be used with caution, because it is based on a single specimen

Extraction of microfossils from the limestone was not successful. The washed residues are mainly composed of blocks of untreated matrix, angular quartz, micas and rare sponge spicules. Extremely rare globular planktonic foraminifera or chambers of foraminifera have been collected but the preservation is poor. Due to their appearance,

accurate identification of these globular specimens is not possible; no tests are preserved or they are still embedded in matrix.

The poverty of foraminiferans in the samples from Wanderfeld IV treated by us contrasts strongly with the abundance and high diversity reported from the locality by McMillan (1992, 2003). Furthermore no ostracods were noticed in our samples, unlike those examined by McMillan (1992).

The sedimentary facies of a bioclastic, carbonate rock with a certain amount of small immature quartz grains and muscovite and a lot of small invertebrate shell fragments, most of which belong to oysters that live on soft sediment, indicates a near-shore environment. The high content of manganese oxide is not extraordinary - manganese is the eleventh most abundant element in the Earth's crust (Anschutz *et al.* 2005). Nevertheless, its occurrence in fairly high amounts at Wanderfeld IV could be due to riverine input in this low-latitude area during the Cretaceous Greenhouse optimum (cf. Hulten *et al.* 2016).

Geological age

The age of the Wanderfeld IV fossils has been debated based on the occurrence of oysters and the, up-to-now, single ammonite specimen. On the basis of *Placenticerias merenskyi* Haughton (1930a) estimated an age not any earlier than “lower Senonian” in accordance with his later writings (Haughton 1930b, 1963, 1969) in which he suggested a “Coniacian” correlation, but in the same paper he considered that the oysters from the same locality denoted a Cenomanian age. Subsequently Martin (1973) and Siesser (1987) accepted a “probably Coniacian” age (both authors referred to Haughton 1930a, 1930b; 1963 and 1969). In contrast, Cooper (1974) suggested a Late Cenomanian age and this was accepted by Howarth (1985), although the latter author questionably assigned the *Pl. merenskyi* type specimen to *Proplacenticerias stantoni* var. *bolli* and referred to the occurrence in Namibia

as Lower Turonian - as for the other occurrences of his *Pro. stantoni* var. *bolli*.

Klinger (1977) as well as Klinger & Kennedy (1989) did not narrow down the age further than Cenomanian and this was basically followed in subsequent text-books and other secondary literature (Tankard *et al.* 1982; Pickford & Senut, 2002; Schneider & Marais, 2004; Pickford & Senut in Schneider, 2008). Cooper (1995) proposed a Cenomanian-Turonian age, and subsequently (Cooper, 2003) the same author narrowed it down to Late Cenomanian - Turonian. The most recent account is also by Cooper (2018) in which he reverted to his 1974 interpretation as Late Cenomanian. These discrepancies make it necessary to discuss the published evidence in detail as well as to add information provided by the new material.

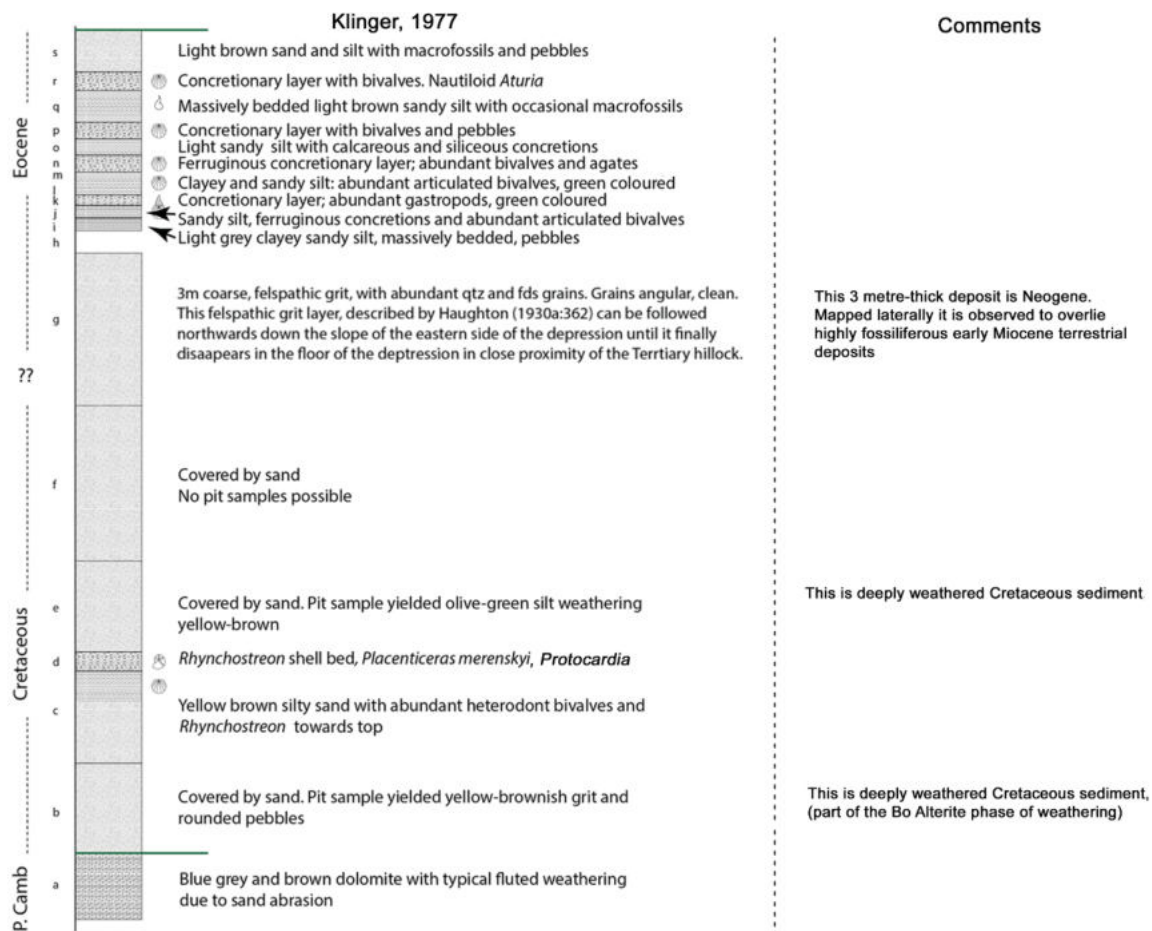


Figure 12. Measured section of the Wanderfeld IV area, modified from Klinger (1977) depicting the shell bed horizon that bears *Rhynchostreon suborbiculatum*, *Protocardia umkwelanensis* and *Placenticerias merenskyi* overlain by Eocene marine deposits and Neogene grits. The grits and silts immediately beneath and above the *Rhynchostreon* shell bed are deeply weathered parts of the Cretaceous deposits (Bo Alterite of Pickford, 2015) as shown by the presence of crumbly ‘ghosts’ of oyster shells in them.

Haughton (1930a) stated that the fossils from near Bogenfels were collected from a Cretaceous section *in situ*. However, it has been debated whether the Cretaceous fossils of Wanderfeld IV were reworked and re-deposited in Palaeogene sediments (Ziegler, 1969). As was pointed out by Klinger (1977: 82) mining operations apparently destroyed most of the section that Haughton (1930b) encountered during his visit to the site and much of the sediment now overlying the bedrock comprises sieved gravel heaps. However, Wanderfeld IV was mined from 1918-1920, well before Haughton's survey. Pickford & Senut (2016) questioned whether Klinger visited the same site as Haughton and they also raised questions about his stratigraphy (Fig. 12). Apart from these uncertainties, the results from the preparation of GSN F1635 clearly indicate that this ammonite was originally embedded in the same matrix as that occurring inside the fossil. Thus the fossil itself has not been reworked into its enclosing matrix for the following three reasons: 1) The filling of the body chamber and the preservation is identical to the surrounding matrix, 2) There was almost no separation between the matrix and the sediment, a reworked fossil would show some sort of separating layer, and 3) The innermost whorls of the right side of the ammonite shell were covered by cementing oysters (*Rhynchostreon*) that were removed during preparation to reveal the ammonite shell. This means that the ammonite was collected from a Cretaceous boulder, independent from the question of whether the Cretaceous deposits are *in situ* or not.

In Cretaceous biostratigraphy, ammonites are the most important macrofossils, with almost 120 index species being used for the "standard" zonal succession of the period (Lehmann, 2015). 80% of these species belong to the regularly coiled suborder Ammonitina – a suborder to which *Placenticer*s spp. belong, but that are not included in that zonation. Although it is obvious that regional biostratigraphic schemes inevitably deviate from the "standard" succession; this hints to the fact that *Placenticer*s is not a taxon comprised of species displaying a high rate of evolution. The genus is widely distributed, but the species in particular intervals are endemic and show a clustered distribution (Bardhan *et al.* 2002). Nevertheless, *Placenticer*s spp. can occasionally be used for biostratigraphic correlations on

a regional scale (Kennedy & Wright, 1983; Kennedy, 1984b; Summesberger, 1985; Summesberger *et al.* 2017). This means that *Placenticer*s *merenskyi* could be of regional stratigraphic value and raises the question whether the combination of shell features permits stratigraphic conclusions for the Wanderfeld IV Cretaceous that is generally agreed to be dated to the Cenomanian, Turonian or Coniacian. The morphologically close *Placenticer*s *kaffrarium* ranges from the Lower to the Middle Coniacian (Kennedy, 1984a; Klinger & Kennedy, 1989). Most of the Middle Coniacian to Santonian species (*Placenticer*s *fritschi*, *Pl. semiornatum*, *Pl. polyopsis* and *Pl. paraplanum*) show a broader to much broader cross section and this feature seems to exclude an age younger than Middle Coniacian for *Pl. merenskyi*. Nevertheless, a small whorl breadth is also encountered in stratigraphically young (Campanian) species such as *Pl. meeki* and *Pl. planum* (Larson *et al.* 1997) and based on the ammonite record alone this does not resolve the uncertainty.

There is a weak case for comparing *Pl. merenskyi* with the European *Pl. memoria-schloenbachi* from the Upper Cenomanian and Turonian, as already mentioned; nevertheless, a generally small cross section and the occurrence of umbilical bullae might correspond to what we know about *Pl. merenskyi* and thus correlation to the Cenomanian or Turonian is possible. Even lower Cenomanian and Upper Albian forms, *Pl. mediasiaticum* and *Pl. kolbajense* (see Kennedy *et al.* 2008) are morphologically so close to *Pl. merenskyi*, that a latest Albian or Lower Cenomanian age cannot be excluded. To summarise, based on our current knowledge of *Pl. merenskyi*, its morphology agrees with a Cenomanian to Coniacian age, but its features are not diagnostic enough to determine a more precise evolutionary level or stratigraphic assignment.

On the basis of associated oysters that are abundant at Wanderfeld IV, Haughton (1930a) estimated an Upper Cenomanian age for the occurrence. He referred to them as *Exogyra* cf. *columba*, whereas Cooper (1974: 87-88) revised the taxonomic assignment of these oysters to *Rhynchostreon suborbiculatum*. Based on beds in southern Angola containing *Rhynchostreon* cf. *suborbiculatum*, Cooper (1974) suggested a late Cenomanian age for the Wanderfeld IV deposit, a view that was accepted by Klinger (1977). Howarth (1985)

discussed the previously published interpretations and accepted an Upper Cenomanian age based on the occurrence of these oysters, referring to “*Exogyra*”, apparently not considering the works by Cooper (1974) and Klinger (1977). Klinger & Kennedy (1989: 349) saw weak evidence for a Late Cenomanian age and thus interpreted the age of that fauna as “Cenomanian?”. Cooper (1995) interpreted *R. suborbiculatum* from Wanderfeld IV as late Cenomanian/Turonian based on the abundance in the well-dated Upper Cenomanian beds of Salinas in Angola (the author had doubts about the identification of the species, since it was not mentioned in the open nomenclature by Cooper 1995: p. 37 in contrast to his 1974 paper) and on interpreting *Pl. merenskyi* as *Placenticerus memoriaeschloenbachi* (see the discussion above).

R. suborbiculatum appears to be locally common to abundant in the Late Cenomanian of many localities in northern to southern Europe (Drahota, 1996; Videt, 2004; Videt & Néraudeau, 2007; Melinte-Dobrinescu *et al.* 2013; Wilmsen, 2017). However, oysters are facies-dependant and this makes stratigraphic conclusions based on frequencies challenging.

For example, salinity changes are believed to be the most important factor explaining why *R. suborbiculatum* is common in the early Cenomanian, fairly rare in the Middle Cenomanian and common in the Upper Cenomanian of southwestern France (Videt & Néraudeau, 2007). As a consequence, this long-ranging species (Upper Albian to Turonian) is cosmopolitan with many records from Africa (Cooper, 1995; Benzaggagh *et al.* 2017; Nagm & Boualem, 2019). The local abundances in the Upper Cenomanian of some areas in Africa and Europe could well be of stratigraphic importance, but ecological preferences might also explain the concentration of oysters at Wanderfeld IV.

Klinger (1977: 87) mentioned that micropalaeontological sampling above and below the *Rhynchostreon* bed (Fig. 12) did not clarify the age of the beds. This is not surprising considering that these deposits are so deeply

weathered that only a few oyster shells remain, represented by friable ‘ghosts’ which crumble when touched.

McMillan (1992, 2003) dated the deposit as early Santonian (Fig. 13). A small fragment of a heteromorph ammonite, reportedly found while processing micropalaeontological samples, was provisionally referred by the author to *Glyptoxoceras?* sp., due to the fact that an early Santonian age was assumed based on abundant planktonic and benthonic foraminiferans and ostracods that he identified (McMillan, 2003; Klinger & McMillan, 2007). The generic assignment of the ammonite (with a question mark) was based on the fact that the fragment shows a convex coiling zone and moderately dense simple ribs. However, if the deposit from which it came is Cenomanian, then identification of the specimen as *Allocrioceras*, which shows the same features, would be plausible (Wippich & Lehmann, 2004).

Due to the scarcity and the poor state of preservation of the microfossils from the site available to the present authors, the planktonic foraminifera from Wanderfeld IV do not provide reliable stratigraphic information, even if the identification of one specimen as *Favusella washitensis*, if correct, would agree with a Cenomanian age. Should the latter be correct, then the correlation by McMillan (1992) of the deposits to the Santonian opens up the possibility that the site yields limestone blocks of diverse ages, throwing doubt on its *in situ* nature (Pickford & Senut, 2016).

We record *Protocardia umkwelanensis*, a cardiid bivalve in the Wanderfeld IV deposit. In general, cardiids are not reliable index fossils, thus the presence of *Pr. umkwelanensis* does not greatly help to refine the stratigraphic position of the Wanderfeld IV occurrence. The species ranges at least from the uppermost Cenomanian (Angola) to the Santonian (South Africa), its common occurrence in the early Coniacian does not permit any further suggestions with respect to the Namibian occurrence.

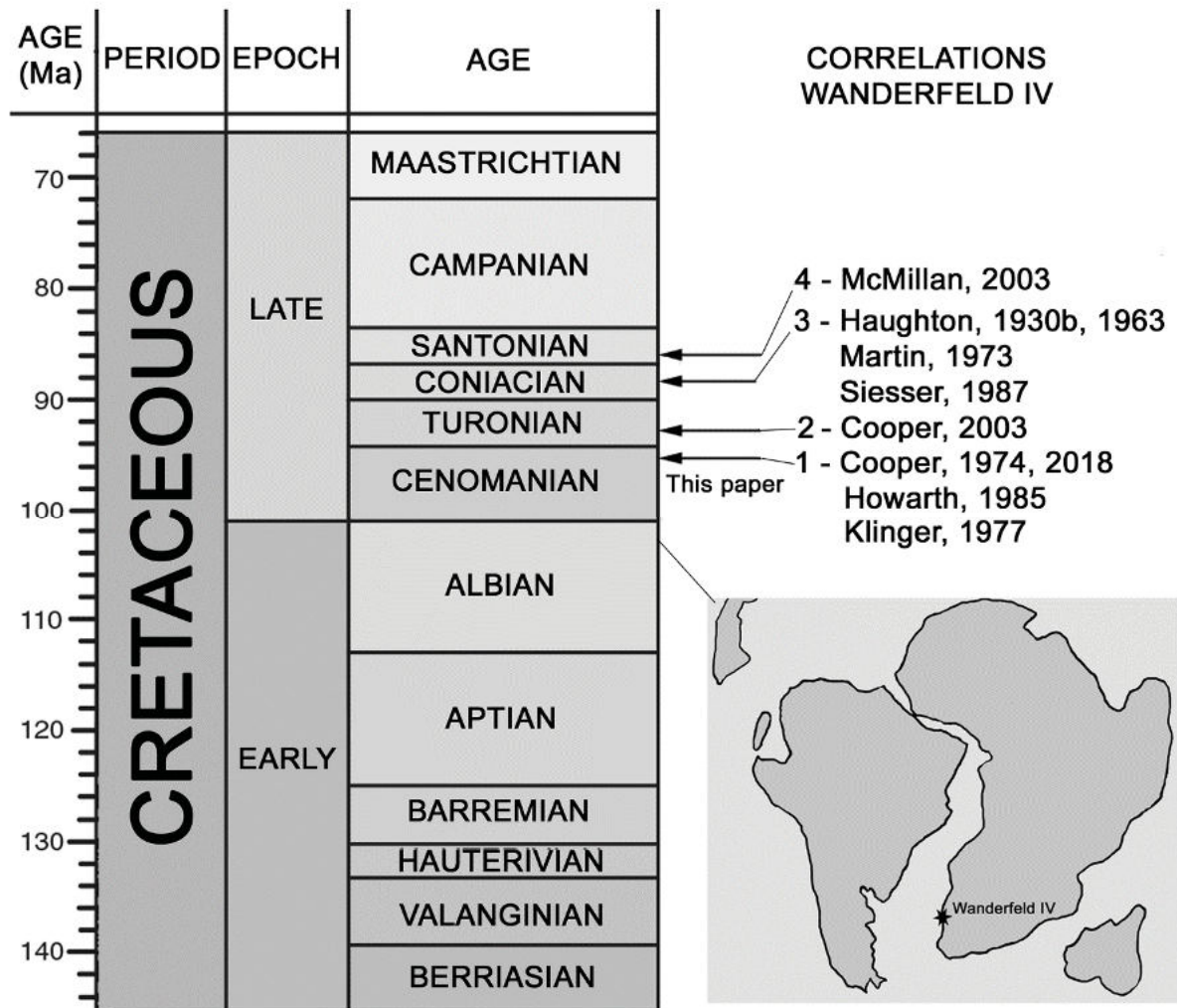


Figure 13. Summary of the main hypotheses about the age of the Wanderfeld IV occurrence. If the identification of *Favusella* is correct, then this would narrow down the possibilities to the Cenomanian, its latest known record being the transition from middle to late Cenomanian. The inset shows the extent of the Atlantic Ocean during the preceding Albian Age. Time scale adapted from Gradstein *et al.* (2012), map outlines based on reconstruction by Pérez-Díaz & Eagles (2014).

Depositional environment

The most striking evidence for the depositional environmental interpretation of the Wanderfeld IV Cretaceous is the abundant occurrence of *Rhynchostreon*. Many of the shells are preserved with both valves, but isolated valves and fragmented fossils are common. Klinger (1977: fig. 6) suggested a *Rhynchostreon* bioherm because of their abundance. *Rhynchostreon* belongs to gryphaeid oysters that are well known as common soft-bottom dwelling recliners on the shelf (Seilacher, 1984; Ayoub-Hannaa & Fürsich, 2011). *Rhynchostreon suborbiculatum* is an abundant species in many regions and is considered to be an eurytopic species and it is only absent from brackish water environments (Videt & Néraudeau, 2007). The partial

destruction of shells prior to burial suggests episodic high water energy during deposition, the macroscopic evidence being confirmed by the bioclastic rock matrix in which there are abundant immature quartz grains. Thus, the abundance of oysters at Wanderfeld IV could partly be due to accumulation by concentration of specimens in a proximal environment. This would also explain the presence of a certain amount of shell debris. The *Rhynchostreon* shell bed of Namibia is thus likely to be an example of an overlapping bioevent *sensu* Wilmsen & Voigt (2006) its deposition having been promoted by the transgression onto the Precambrian basement, a near-shore dynamic palaeoenvironment and a preservational milieu favourable for calcitic shells. Similar mass

occurrences are known from many regions in the world (Drahota, 1996; Melinte-Dobrinescu *et al.* 2013; Wilmsen, 2017). A less prominent example of gryphaeid mass occurrences is the *Pycnodonte* Event in North Germany that demonstrates that there are greater numbers of oyster fossils in proximal positions of the shelf compared to distal positions (Wilmsen & Voigt, 2006).

This environmental interpretation agrees with the foraminiferal record. As

planktonic foraminiferans are rare and exclusively globular, it is concluded that the Wanderfeld IV environment was not favourable for their proliferation and diversification, on which basis we infer that the deposits were likely to have accumulated in a proximal setting. This inference agrees with the presence of *Favusella* that is suited to shallow, warm, hypersaline and carbonate-saturated environments (Dias-Brito, 1982; Koutsoukos *et al.* 1989).

Conclusions

The locality of Wanderfeld IV in the Sperrgebiet, Namibia, has yielded abundant oyster fossils, four specimens of ammonites (two of which are reasonably well preserved) and rare cardiid bivalves. The limestones that enclose the fossils contain small angular quartz grains as well as occasional large (up to 5 cm diameter) well-rounded quartz pebbles, indicating a shallow marine proximal depositional environment. The deposit is clearly late Cretaceous, but there is some hesitation concerning its precise position within this epoch. The combined evidence of the ammonite specimens, the oysters and the cardiid, as well as some poorly preserved foraminiferans, suggests correlation to the Cenomanian

although a Turonian or Coniacian correlation cannot be ruled out. Correlation to the Santonian (McMillan, 1992, 2003) is not supported by the new fossil material.

If the identification of *Favusella* is correct, then a Cenomanian correlation would be likely (Fig. 13) because the latest record of this genus is the transition between the middle and late Cenomanian.

The depositional environment is considered to have been close to the palaeo-shoreline of the nascent Atlantic Ocean in a relatively high energy, proximal location (Fig. 13) possibly reflecting a transgressive phase. If so then a late Cenomanian correlation would be most likely.

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We dedicate this paper to our colleague Luc Bulot (Manchester University) who has published extensively on Cretaceous ammonites, biogeography and stratigraphy.

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