New considerations on dimorphism and aptychus in *Gravesia* Salfeld (Ammonoidea; Late Jurassic)

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With 6 figures


Abstract: Recent findings of *Gravesia gravesiana* (d'Orbigny) from the Lower Tithonian (Hybonotum Zone, *laisackerensis* Horizon) of Liptingen (SW Germany) indicate the presence of dimorphism in the genus *Gravesia* Salfeld in which the dimorphic partners differ significantly in their mouth borders. A new type of aptychus occurring in the same beds most likely corresponds to *Gravesia*. The systematic position of *Gravesia* is briefly discussed.


1. Introduction

Since the first description of a specimen of the ammonite genus *Gravesia* Salfeld, 1913 – *Ammonites gigas* – from the Jurassic of SW Germany by Zieten (1830), this genus is often used as an important guide fossil in the marine Upper Jurassic deposits of North-western and Central Europe ("biome franco-germanique" sensu Hantzpergue 1989). The palaeobiogeographic distribution of *Gravesia* together with biostratigraphical data was discussed and summarized in papers by Hahn (1963), Hantzpergue (1989), and Schweigert (1993a, b, 1996b, 1999). Further information...
Fig. 1. Provenance of the studied ammonite material in the Upper Jurassic of SW Germany.

Fig. 2. The Hangende Bankkalke Formation (Tithonian, Hybonotum Zone, laisakkerensis Horizon) exposed in the Liptingen quarry. The rich ammonite fauna comes from the bedded limestones close to a large sponge-microbial reef complex (right). The limestones are partly deformed by olistoliths (center) from the neighbouring reef.

Despite the existence of numerous nicely preserved specimens of *Gravesia* collected bed-by-bed in the latest Kimmeridgian and early Tithonian of W France, NW Germany and S Germany, little was known about dimorphism in this genus. HAHN (1963) spoke of small, “microgerontic” specimens within a large variation of adult sizes, but did not at all consider sexual dimorphism.

HANTZPERGUÉ (1987) asserted that presumably adult specimens showing a relatively small diameter represent microconchs, and larger specimens were the corresponding macroconchs. He separated these two dimorphs based on different growth and ribbing curves. SCHWEIGERT (1996a) followed this view of HANTZPERGUÉ and distinguished in faunal lists between macroconchs [M] and microconchs [m], but none of this material was illustrated yet.

Also the aptychi corresponding to *Gravesia* were almost unknown. HAHN (1963: 96) mentioned a specimen of *Gravesia* from Boulogne-sur-Mer in the collection of the University of Tübingen which exhibits the negative print of the convex side of an aptychus close to the aperture so that he assumed this aptychus could belong to this ammonite. The counterpart of this specimen was said to be preserved too (HAHN 1963).

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New findings from the Lower Tithonian Hangende Bankkalke Formation (Hybonotum Zone, *laisackerensis* Horizon) exposed in a large quarry near Liptingen (SW Germany; Figs. 1-2) provide interesting information both concerning dimorphism and the presumed aptychus of *Gravesia*. Previous results on biostratigraphy, lithology, economic aspects and the ammonite *Aptychus* could belong to this ammonite. The counterpart of this specimen was said to be preserved too (HAHN 1963).

Additional material for comparisons and statistical evaluations is housed at the University Erlangen-Nürnberg (most material mentioned in the thesis of M. DIMKE) and in the private collections of one of the authors (A. S.), and of the firm MEICHLE & MOHR (Immenstaad, Germany).

Abbreviations: [M] = macroconchiate form; [m] = microconchiate form.

1996* Gravesia gravesiana*. – HAHN, p. 101, pl. 11, fig. 1 only.

2. Material
The figured specimens are deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS). Additional material for comparisons and statistics is housed at the University Erlangen-Nürnberg (most material mentioned in the thesis of M. DIMKE) and in the private collections of one of the authors (A. S.), and of the firm MEICHLE & MOHR (Immenstaad, Germany).

Abbreviations: [M] = macroconchiate form; [m] = microconchiate form.

3. Systematic palaeontology
Superfamily Perisphinctoidea STEINMANN in STEINMANN & DÖDERLEIN, 1890
Family incertae sedis
Subfamily Gravesiinae ZEISS in FISCHER & ZEISS, 1987
Genus *Gravesia* SALFELD, 1913

*Gravesia gravesiana* (d'ORBIGNY, 1847). Fig. 3

- 1847 *Ammonites gravesianus* d'ORBIGNY, p. 559, pl. 219, figs. 1-2.
- 1915 *Holocostephanus* (Gravesia, SALFELD) *Gravesianus* d'ORB. – SCHNEID, S. 166, pl. 7, fig. 1. [= G. gigas]
1959 *Gravesia gravesiana* (d'ORBIGNY). – ZEISS, p. 13, fig. 2 only.
1963 *Gravesia gravesiana*. – HAHN, p. 99, pl. 10, figs. 3-4, pl. 13, fig. 2 only.
1963 *Gravesia polyleura* n. sp. – HAHN, p. 101, pl. 11, fig. 1 only.
1987 *Gravesia gravesiana*. – HAHN, p. 101, pl. 11, fig. 1 only.
1997 *Gravesia gravesiana*. – ZEISS et al., p. 77ff., pl. 11, fig. 1.

*Gravesia gravesiana*. – ZEISS et al., p. 77ff., pl. 11, fig. 2, pl. 12, fig. 2.

Studied material: More than 50 specimens from the Hangende Bankkalke Formation (Lower Tithonian, Hybonotum Zone, *laisackerensis* Horizon) of the western part of the Swabian Alb, SW Germany; illustrated specimen (Fig. 3) SMNS 66204.
Fig. 3. *Gravesia gravesiana* (d’ORBIGNY) [M], Lower Tithonian, KWV Jura-Steinwerke Liptingen; Hangende Bankkalke Formation, Hybonotum Zone, laiskkerensis Horizon (SMNS 66204, leg. A. SCHERZINGER). – Maximum measurable diameter of fragment 176 mm.

Description: The figured specimen is a slightly compressed steinkern, which shows already in the inner whorls a moderately dense, coarse, bipartite – polygyrate ribbing with a diverging point of the ribs close to the funnel-shaped umbilicus. On the body-chamber the ribs become wider-spaced and more irregularly arranged. Just behind the aperture the ribbing is very weak. The secondary ribs are crossing the venter without interruption or weakening. The whorl section is broadly oval – coronate in all discernible ontogenetic stages. The peristome is formed by a rounded, collar-shaped swelling. In the figured specimen it is only partly preserved on the figured side of the flank, up to the middle of the venter. The rest of the peristome was probably broken off during transport, before the burial of the shell.

Remarks: According to the observations below, we interpret the examples of *Gravesia* taken by HANTZPERGUE (1989) as microconchiate forms more likely represent small macroconchs. In the previously described macroconchiate specimens of *Gravesia* (HANTZPERGUE 1989) the shells are incompletely preserved, lacking the final mouth border and thus provide a misleading impression of the true shape of the peristome. We suspect the very thin-shelled apertural peristomes are mostly broken away before the specimens were embedded. Similar collar-shaped peristomes occur in several stephanoceratid ammonite genera from the Middle Jurassic (*Stephanoceras, Emileia, Eryctites*, see e.g. ARKELL 1957).

Our studies of plenty of specimens of *Gravesia gigas* (ZIETEN) and *G. gravesiana* (d’ORBIGNY) from the Lower Tithonian of (S and NW) Germany as well as more than 50 specimens of *G. iarius* (d’ORBIGNY) from the Upper Kimmeridgian of Holzen/Ith (NW Germany) revealed that macroconch specimens are highly variable concerning their final diameters, their individual onset of ontogenetic stages, whorl heights, whorl widths, and umbilical widths. The ribbing curves and growth parameters on which HANTZPERGUE (1987, 1989) separated microconchiate and macroconchiate forms of *Gravesia* plot very close to each other and in our view lie within the intraspecific variation of macroconchs. With only few specimens available from one and the same bed a larger specific diversity might be suspected. One of the smallest recorded adult specimens showing a characteristic macroconchiate peristome (Fig. 3) is not bigger than the herein recorded macroconch (Fig. 4); their final diameters are both less than 200 mm. The maximum recorded diameter of macroconchs reaches more than 500 mm. In larger macroconch specimens the body-chamber becomes smooth in the adult stage.

The biostratigraphic dating of locations only based on single, juvenile or poorly preserved specimens of *Gravesia* is often problematic. Specimens mentioned by ZEISS et al. (1996) as ‘*Gravesia gigas intermedia*’ and later figured by DIMKE & ZEISS (1997) from Liptingen and a specimen mentioned from Geistermühle quarry near Heudorf im Hegau (ZEISS et al. 1996) fall into the variability of *Gravesia gravesiana* (d’ORBIGNY).

**Gravesia gravesiana** (d’ORBIGNY) [m]

non 1987 *Gravesia gravesiana* (d’ORBIGNY). – HANTZPERGUE, p. 247 f., pl. 19, fig. a [= macroconch form].

non 1989 *Gravesia gravesiana* (d’ORBIGNY). – HANTZPERGUE, p. 206 f., 210 f., fig. 54h, figs. 55-56 pars, pl. 19, fig. a [= macroconch form].

non 1996a *Gravesia gravesiana* (d’ORBIGNY) [m]. – SCHWEIGERT, p. 298. On 1987 *Gravesia gravesiana* (d’ORBIGNY) – HANTZPERGUE, p. 247 f., pl. 19, fig. a [= macroconch form].

**Gravesia gravesiana** (d’ORBIGNY) [m] Fig. 4

Studied material: 1 complete specimen from the Hangende Bankkalke Formation (Hybonotum Zone, laiskkerensis Horizon) of Liptingen, SW Germany (Coll. SCHERZINGER, SMNS no. 66205), 1 incomplete additional specimen from the same locality (Coll. SCHERZINGER).
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Fig. 4. Gravesia gravesiana (d’Orbigny) [m], Lower Tithonian, Hangende Bankkalke Formation, KWV Jura-Steinwerke Liptingen; Hybonotum Zone, laisackerensis Horizon (SMNS 66205, leg. A. SCHERZINGER). – Maximum diameter 180 mm.

**Description:** The single complete specimen is a slightly compressed steinkern, which exhibits already on the inner whorls a moderately dense, coarse, bipartite ribbing with a very low diverging point, located at the maximum width, thus leading to coronate morphology. On the body-chamber the ribs become wider-spaced and more irregularly arranged. Few single ribs occur in the area of weak constrictions. The final ribbing stage consists of slightly retrocostate units. The ribs are crossing the venter without any interruptions. During ontogeny the whorl section is first broad-oval, then becomes coronate, and finally high-oval. Towards the aperture the shell becomes more evolute, and the coiling of the last whorl is slightly eccentric also indicating that the specimen was adult. Close to the mouth border a shallow constriction is developed. Sinauous aperture margins are preserved on both flanks. In the ventral part of the aperture, a liplike extension occurs.

**Comparisons:** In macroconch specimens of *Gravesia gravesiana* the whorl section of the medium and final stage is more rounded, much more involute, and broader than in the corresponding microconch. At equal diameters tripartite ribbing units occur besides biplicate ones only in the macroconchs. In large macroconchs the body-chamber is smooth and the peristome plain.

The coeval *Tolvericeras gravesiforme* Hantzpergue exhibits a broad, rounded whorl section, and its coiling is much more evolute than both in *Gravesia gravesiana* [M] (see Hantzpergue 1989) and corresponding [m] (this study). Although the ribbing style is also bipartite the ribs are more distantly arranged on the adult body-chamber. In microconch specimens of *Tolvericeras tolvense* Hantzpergue from the early Late Kimmeridgian large, stalked lappets are developed at the peristome (Hantzpergue 1989, fig. 33c, pl. 11, fig. a). In other species of this genus the peristome of microconch specimens is not yet recorded.

**Remarks:** Consequently, in other chronospecies of the genus *Gravesia* a homologous dimorphism must be considered. Such candidates for microconchs are expected to have a coarse and wide-spaced, mostly biplicate ribbing style. Possibly the strongly crushed specimens from the Paris Basin termed as “Episphinctoceras horridum” by Maubeuge (1996) could represent such microconchs corresponding to *Gravesia gigas* (Zieten).

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4. The aptychus of the ammonite genus *Gravesia* Salfeld

Hitherto the only record of an aptychus probably belonging to *Gravesia* was mentioned by Hahn (1963). This aptychus was embedded close to the mouth border of a *Gravesia gigas* from Boulogne-sur-Mer. He interpreted this form as belonging to the form-genus *Praestriaptychus* Trauth because of the lacking of spines or other ornamentation, but did not give an illustration. Unfortunately this specimen is not traceable in the collection of Tubingen University.

During a field trip to the Liptingen quarry in summer 2005 (H.P., A.S.) a very large but fragmented (probably bitten) aptychus (Figs. 5-6) was discovered in a loose block fallen down from the wall of the quarry including the aptychus fauna of the *laisackerensis* Horizon. The enormous size and especially the width of this incomplete aptychus indicate that it most likely stems from a very large ammonite with a broad whorl section. In the aptychus fauna of the *laisackerensis* Horizon from this locality at least four other large-growing perisphinctid genera are recorded besides *Gravesia gravesiana* (d’Orbigny): *Eiwigalithacoceras* Zeiss, Schweigert & Scherzinger, *Lithacoceras* Hyatt s.l., *Hegovisphinctes* Zeiss, Schweigert & Scherzinger.
Fig. 5. Fragment of an aptychus probably belonging to *Gravesia gravesiana* (d'ORBIGNY), Lower Tithonian, Hangende Bankkalke Formation, KWV Jura-Steinwerke Liptingen; Hybonotum Zone, *laisackerensis* Horizon (SMNS 66206, leg. H. PARENT). – Width of photograph 165 mm.

GERT & SCHERZINGER, and HOELDERIA OHMERT & ZEISS. They are all unequivocal perispinctids which differ from *Gravesia* by their high-oval, not coronate whorl sections. In Upper Jurassic perispinctids either a Praestriaptychus or a Strigogranulaptychus occurs (see TRAUTH 1937; SCHWEIGERT & DIETL 1999; SCHWEIGERT 2000). Strigogranulaptychus was considered as synonymous with Granulaptychus by ENGESER & KEUPP (2002). The aspidoceratid genera Physodoceras HYATT and Aspidoceras ZITTEL both exhibit a broad-oval whorl section and, like all other aspidoceratids, another type of aptychus, which is well-known as form-genus Laevaptychus TRAUTH (see SCHINDEWOLF 1958; SCHWEIGERT & SCHERZINGER 1997; SCHWEIGERT 1998; SCHWEIGERT & DIETL 2001). Despite of the
fragmentary preservation of the aptychus from Liptingen it is well discernible that the convex side exhibits broad sinuous folds where the aptychus is widened up and shows a porous, bone-like internal structure. The lateral margins of this aptychus are very thin, in striking contrast to Laevaptychus, in which the maximum thickness is always developed along the margins. The concave surface of the aptychus fragment from Liptingen bears irregular growth lines, sometimes with a weak linear punctuation unknown from other form-genera of aptychi.

5. Systematic position of Gravesia

Both the palaeobiogeographic origin and phyletic derivation of Gravesia is unclear and still a case of debate. Following Hahn (1963) we exclude a derivation of Gravesia from the genus Aulacostephanus Sutner & Pompecki in Tornquist, as it was later proposed by Zeiss (1968). In the latter, a long, slender, tongue-shaped lappet is developed in the microconchs, and the whorls section is never coronate (Ziegler 1962). Zeiss (1968) published a small specimen of an aulacostephanoceratid from the Upper Kimmeridgian of Franconia and interpreted this specimen as a possible phyletic link between Aulacostephanus and Gravesia. Most likely this specimen is a nucleus of Aulacostephanus coniejanei (Thurmann). The latter species, used as an index species of a faunial biohorizon in the higher part of the French Eudoxus Zone (Hantzpergue 1989) was also recorded from Swabia, Russia, and NW Germany (see Schweigert 1996b; Hantzpergue et al. 1998a, b; Scherzinger & Mitta, this volume). For a recent overview on the very rare findings of aulacostephanoceratids see Schweigert & Vallon (2005).

From the Kimmeridgian of Lower Saxony Fischer & Zeiss (1987) described a new monotypic genus Praegravesia Zeiss, which was placed in the newly founded subfamily Gravesiinae Zeiss within Aulacostephanidae Spath. The recovery circumstances of the two specimens of Praegravesia rolkei are somewhat obscure, and it appears very likely that they were reworked from the Middle Jurassic (Schweigert 1999), or they come from another locality. According to local collectors' intimate knowledge of the Jurassic of the vicinity of Wolfsburg, the two specimens never came from this area (oral communication by F.-D. Paul, Wolfsburg). For the separation of the genus Gravesia from other perisphinctoids, we may anyway use the subfamily Gravesiinae. This, however, tells nothing about its systematic affiliation on family level.

Hantzpergue (1989) suggested a common ancestry of Gravesia and his newly introduced genus Tolvericeras. Indeed there are some similarities between Tolvericeras Hantzpergue and Gravesia Salfeld. The stratigraphically oldest known chronospecies of Gravesia, G. lafauriana Hantzper-
valved apycthus of unclear affinity from the Upper Kimmeridgian Nuspli- 
gen Lithographic Limestone, which was at that time tentatively assigned to 
Aulacostephanus, although this genus is otherwise not recorded from this 
formation, and thus the questionable apycthus more likely belongs either to 
Ochetoceras Hau or to Streblites Hyatt.

6. Conclusions

In the Tithonian ammonite species Gravesia gravesiana (b’Orbigny) di- 
morphism affecting the peristome is reported for the first time. A complete 
specimen described herein is the first unequivocal record of a microconch 
Gravesia. All specimens previously figured or mentioned in faunal lists as 
macroconch specimens of Gravesia (Hantzpergue 1989; Schwiegert 
1996a) are doubtful and in our view more likely represent small macro- 
conchs.

The existence of a very large apycthus most probably belonging to 
Gravesia may provide hints for its systematic placement. Since it is strik- 
ingly different from typical Praestriaptychus, the assignment of Gravesia to 
a separate subfamily within Perisphinctoidea is strongly supported, although 
its closer relatives are still unknown and thus its ancestry remains enigmatic.

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