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.

**Zusammenfassung:** Neufunde von *Gravesia gravesiana* (d’Orbigny) aus dem Unter-Tithonium (Hybonotum-Zone, laisackerensis-Horizont) von Liptingen (Südwestdeutschland) belegen die Existenz eines Dimorphismus bei der Gattung *Gravesia SALFELD*, wobei sich die beiden dimorphen Partner insbesondere hinsichtlich ihrer Mündung deutlich voneinander unterscheiden. Ein neuer Formtyp eines Aptychus aus denselben Fundschichten dürfte zu *Gravesia* gehören. Die systematische Stellung dieser Gattung wird kurz diskutiert.

**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, laisakerensis 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.
may be obtained from BERCKHEMER & HÖLDER (1959), ZIEGLER (1960),
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.
HANTZPERGUE (1987, 1989) asserted that presumably adult specimens
showing a relatively small diameter represent microconchs, and larger speci-
mens were the corresponding macroconchs. He separated these two di-
morphs based on different growth and ribbing curves. SCHWEIGERT
(1996a) followed this view of HANTZPERGUE and distinguished in faunal
lists between macroconchs [M] and microconchs [m], but none of this
material was illustrated yet.

Also the aptchi 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 aptchus close to the aperture so that he assumed this
aptchus could belong to this ammonite. The counterpart of this specimen
was said to be preserved too (HAHN 1963).

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 aptchus of *Gravesia*. Previous
results on biostratigraphy, lithology, economic aspects and the ammonite
fauna of this locality were published by ZEISS (1994), SCHWEIGERT (1996a),
ZEISS et al. (1996), DIMKE (1997), and DIMKE & ZEISS (1997).

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 MEICHL & MOHR (Immenstaad, Germany).

Abbreviations: [M] = macroconchiat form; [m] = microconchiat form.
3. Systematic palaeontology

Superfamily Perisphinctoidea STEINMANN in STEINMANN & DÖDERLEIN, 1890
Family incertae sedis
Subfamily Gravesiinae ZEISS in FISCHER & ZEISS, 1987
Genus Gravlesia SALFELD, 1913

Type species: Ammonites gravesianus d’ORBIGNY, 1847.
Included species: Ammonites gigas ZIETEN, 1830; Ammonites gravesianus d’ORBIGNY, 1847; Ammonites irius d’ORBIGNY, 1847; Gravlesia laiauriana HANTZPERGUE, 1987 (for synonymy see HANTZPERGUE 1989).

Gravlesia gravesiana (d’ORBIGNY) [M] Fig. 3

* 1847 Ammonites Gravesianus d’ORBIGNY, p. 559, pl. 219, figs. 1-2.
non 1915 Holcostephanus (Gravlesia, SALFELD) Gravesianus d’ORB. – SCHNEID, S. 166, pl. 7, fig. 1. [= G. gigas]
1963 Gravlesia gravesiana (d’ORBIGNY). – HAHN, p. 99, pl. 10, figs. 3-4, pl. 13, fig. 2 only.
1963 Gravlesia polypleura n. sp. – HAHN, p. 101, pl. 11, fig. 1 only.
non 1974 Gravlesia sp. – ZAKHAROV & MESEZHKINOV, p. 177, pl. 1, fig. 2.
1989 Gravlesia gravesiana (d’ORBIGNY). – HANTZPERGUE, p. 205, pl. 19, figs. a-c. [with list of further synonymy]
1997 Gravlesia gigas intermedia HANTZPERGUE. – DIMKE & ZEISS, p. 77ff., pl. 11, fig. 1.
1997 Gravlesia gravesiana (d’ORBIGNY). – DIMKE & ZEISS, p. 77ff., pl. 11, fig. 2, pl. 12, fig. 2.
1999 Gravlesia gravesiana. – SCHWEIGERT, p. 35f.

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. Gravestia gravesiana (d'Orbigny) [M], Lower Tithonian, KWV Jura-Steinwerke Liptingen; Hangende Bankkalke Formation, Hybonotum Zone, laisakkerensis 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, Erycites*, 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. irius* (d’Orbigny) from the Upper Kimmeridgian of Holzeln/Oth (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 corresponding microconch (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 Dmke & Zeiss (1997) from Liptingen and a specimen mentioned from Geister-müthle 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.

Studied material: 1 complete specimen from the Hangende Bankkalke Formation (Hybonotum Zone, latisackerensis Horizon) of Liptingen, SW Germany (Coll. Scherzinger, SMNS no. 66205), 1 incomplete additional specimen from the same locality (Coll. Scherzinger).
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. Sinuous aperture margins are preserved on both flanks. In the ventral part of the aperture, a lip-like 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 bicipitate ones only in the macroconchs. In large macroconchs the body-chamber is smooth and the peristome plain.

The coeval *Toliviceras gravesiforme* Hantzperge exhibits a broad, rounded whorl section, and its coiling is much more evolute than both in *Gravesia gravesiana* [M] (see Hantzperg 1989) and corresponding [in] (this study). Although the ribbing style is also bicipitate the ribs are more distantly arranged on the adult body-chamber. In microconch specimens of *Toliviceras tolierense* Hantzperg from the early Late Kimmeridgian large, stalked lappets are developed at the peristome (Hantzperg 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 bicipitate ribbing style. Possibly the strongly crushed specimens from the Paris Basin termed as "Episphinctoceras horridum" by Maubouge (1996) could represent such microconchs corresponding to *Gravesia gigas* (Zetter).

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 *Praesutriaptychus 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 Tübingen 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 ammonite 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 ammonite fauna of the *laisackerensis* Horizon from this locality at least four other large-growing perisphinctid genera are recorded besides *Gravesia gravesiana* (d’Orbigny): *Euvirgilithacoceras* Zeiss, *Schweigert & Scherzinger, Lithacoceras Hyatt s.l.*, *Hegovisphinctes* Zeiss, Schwei-
Fig. 5. Fragment of an aptychus probably belonging to *Gravestia gravesiana* (d’Orbigny), Lower Tithonian, Hangende Bankkalke Formation, KWV Jura-Steinwerke Liptingen; Hybonotum Zone, *taisackerensis* Horizon (SMNS 66206, leg. H. Parent). – Width of photograph 165 mm.

GERT & SCHERZINGER, and HOELDERIA OHMERT & ZEISS. They are all unequivocal perispininctids which differ from *Gravesia* by their high-oval, not coronate whorl sections. In Upper Jurassic perispininctids either a *Praestriaptychus* or a *Strigogranulaptychus* occurs (see TRAUT 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* TRAUT (see SCHINDEWOLF 1958; SCHWEIGERT & SCHERZINGER 1997; SCHWEIGERT 1998; SCHWEIGERT & DIETL 2001). Despite of the
Fig. 6. Detail of aptchus fragment from Fig. 5.
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 & Pompeckj in Tornquist, as it was later proposed by Zeiss (1968). In the latter, a long, slender, tongue-shaped lappend 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 contejeani* (Thurmann). The latter species, used as an index species of a faunal biohorizon in the higher part of the French Eudoxus Zone (Hantzpergue 1989) was also recorded from Swabia, Russia, and NW Germany (see Schweigert 1996; Hantzpergue et al. 1998a, b; Scherzinger & Mitza, this volume). For a recent overview on the very rare findings of aulacostephanids in the late Upper Kimmeridgian of SW Germany 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 perispincoiids, 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. lafiuriana* Hantzper-
GUE still exhibits a rather evolute coiling and a coarse bicipitate ribbing of the juvenile whorls. In Tolvericeras, however, a typical perispininctid lappet is developed in the microconchs thus contrasting the herein recorded sinuous peristomial morphology in a microconch Gravesia. This may contradict a derivation of Gravesia SALFELD from Tolvericeras HANTZPERGUE, although such a morphological change with a disappearance of lappets during phylogeny cannot be excluded and is also reported form other Late Jurassic perispininctid genera (e.g. Propectinatites COPE, 1968 – Pectinatites BUCKMAN, 1922).

Callomon (in Donovan et al. 1981) suggested a phyletic derivation of Gravesia from the Early Kimmeridgian group of Eurasenia trimera (Oppel) [M] – Prorasenia stephanoides (Oppel) [M]. In this dimorphic couple, however, the size ration between large macroconchs and rather minute microconchs is much different from that in Gravesia, and also in Prorasenia long, well-developed lappets occur.

The genus Metagravesia Spath was first described from Kachchh (Spath 1931) and otherwise only recorded from Pakistan (Fatmi & Zeiss 1999). There is some resemblance of this rather evolute form with Gravesia lafauriana Hantzpergue from the late Kimmeridgian, which is the stratigraphically oldest undoubted species of Gravesia. However, the long palaeobiogeographic distance and significant differences in their suture lines exclude a derivation of Gravesia from Metagravesia.

Specimens of ‘Gravesia’ reported from the Upper Jurassic of NW Siberia (Zakharov & Mezeghnkov 1974; Mezeghnkov 1984) are highly questionable and more likely represent homoeomorphic perispininctoids, especially in respect of their different suture lines, with a very characteristic umbilical lobe U₁. Gravesia (?) triplicata Mezeghnkov, 1963 from the Subpolar Ural, only tentatively included in the genus, exhibits a much more evolute style of coiling, a finer ribbing, and differences in its suture line. Later this species was correctly assigned to Eosphinctoceras Mezeghnkov, 1974 (see Zakharov & Mezeghnkov 1974: 88). Also the presence of an endemic species of Gravesia in the Upper Jurassic of East Africa and Madagascar cannot be confirmed. The specimens of ‘Gravesia’ loupekihei published by Verma & Westermann (1984) from the Kimmeridgian/Tithonian boundary beds of Kenya represent an offshoot of katolriceratids which differs from Gravesia e.g. in a different suture line and a different ontogeny. Both the shape of the peristome and the aptychus are unknown in the African species.

Another hint to evaluate the systematic position of Gravesia may be obtained from the corresponding aptychus. At present, similar forms are unknown. The aptychi of aulacostephanids, raseniids, and of katolriceratids, are still unknown too. Schweigert & Scherzinger (1997) and Schweigert (1998) recorded the single isolate specimen of a high-rectangular, thin-
valved aptychus of unclear affinity from the Upper Kimmeridgian Nusplingen 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 aptychus more likely belongs either to *Ochetoceras* HAUG or to *Streblites* HYATT.

6. Conclusions

In the Tithonian ammonite species *Gravesia gravesiana* (d'ORBIGNY) dimorphism 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 microconch specimens of *Gravesia* (HANTZPERGUE 1989; SCHWEIGERT 1996a) are doubtful and in our view more likely represent small macroconchs. The existence of a very large aptychus most probably belonging to *Gravesia* may provide hints for its systematic placement. Since it is strikingly different from typical *Praestriapecthus*, 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.

Acknowledgements

Many thanks for fruitful discussions, rare literature and valuable advice go to Prof. Dr. J. H. CALLON, London, Dr. G. DIETL, Stuttgart, Dr. V. V. MITTA, Dr. M. ROGOV, both Moscow, and V. DIETZE, Riesburg. Moreover, we wish to thank Dr. R. MOHR (MEICHLE & MOHR, Immenstaad), H.-J. RÖTTGER, W. UMHAUER, E. STRAUB, and G. RIEGER (KWV Jura-Steinwerke Liptingen) for their permission and permanent support of our studies in the Liptingen quarry. F.-D. PAUL (Wolfsburg) provided useful information on the provenance of *Praegravesia rolkei*. Dr. H. SCHULZ (Institut für Geowissenschaften, University of Tübingen) is thanked for providing access to the collection. Dr. E. MÖNNING (Coburg) is thanked for a joint trip to the collections of the Geologische Bundesanstalt Hannover, and the museum of the Institut für Geowissenschaften, University of Göttingen, where numerous specimens of *Gravesia* from NW Germany are housed. Dr. G. DIETL (Stuttgart) and Prof. Dr. R. ENAY (Villeurbanne) are thanked for their critical comments and valuable suggestions on an earlier draft of this paper.

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Manuscript received: January 24th, 2006.
Revised version accepted: June 26th, 2006.

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