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

Armin Scherzinger, Immendingen-Hattingen, **Günter Schweigert,** Stuttgart, and **Horacio Parent,** Rosario

With 6 figures

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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

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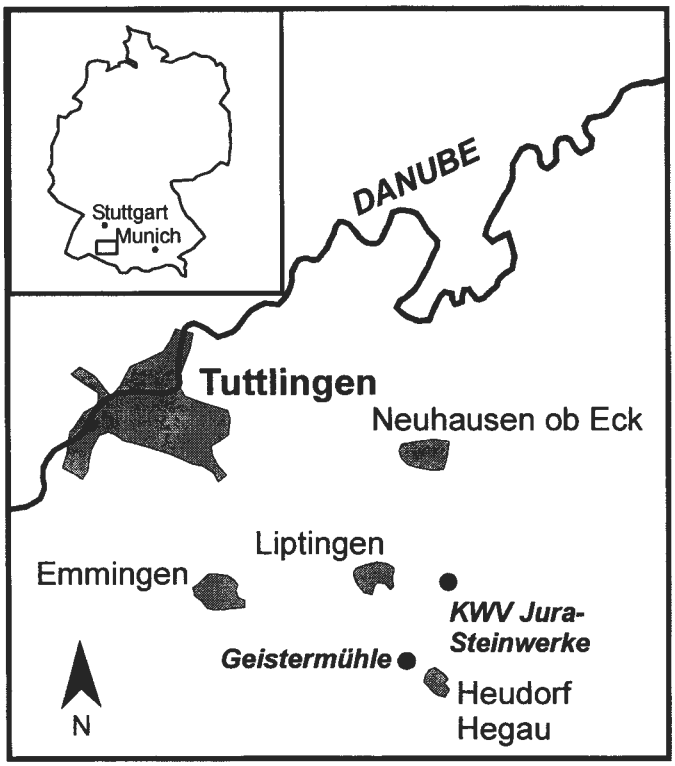
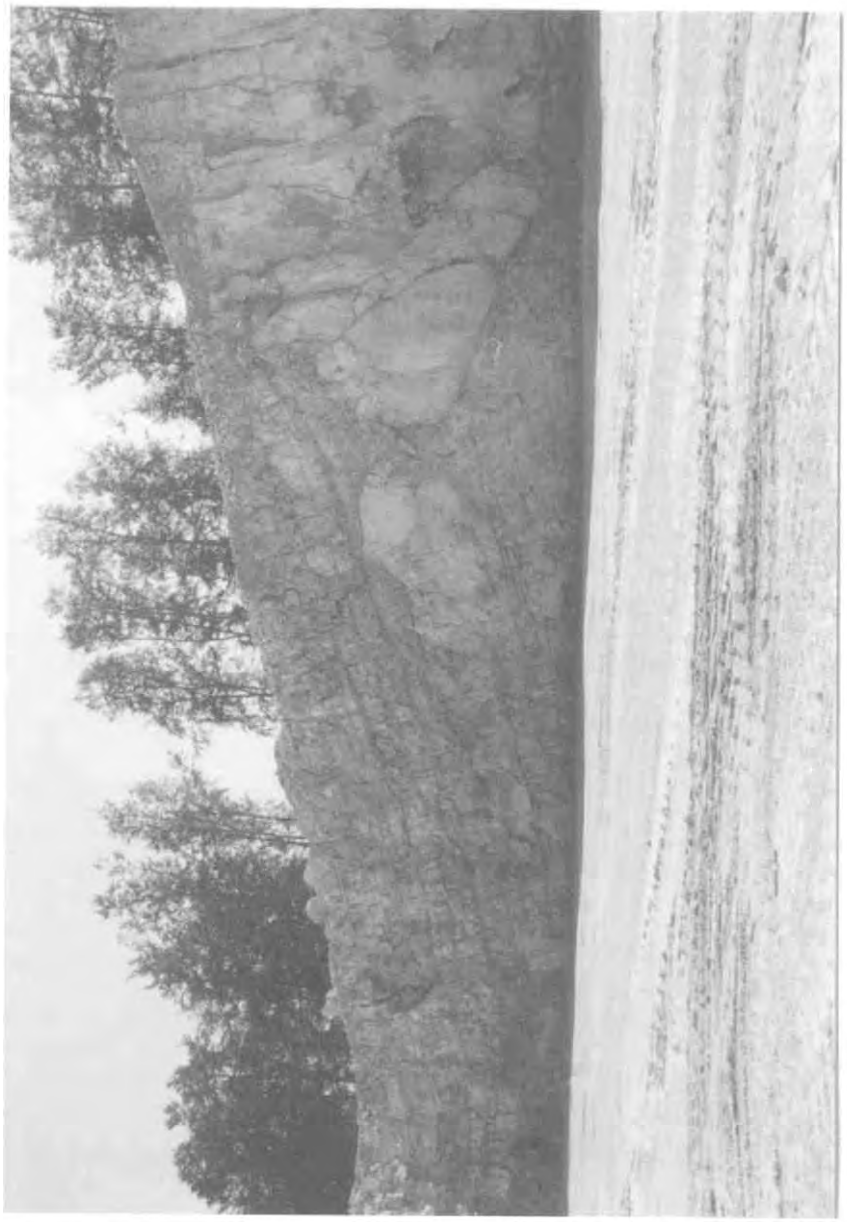


Fig. 1. Provenance of the studied ammonite material in the Upper Jurassic of SW Germany.

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 olistholiths (center) from the neighbouring reef.



may be obtained from BERCKHEMER & HÖLDER (1959), ZIEGLER (1960), ZEISS (1964), COPE (1967), ENAY (1966), MAUBEUGE (1971, 1996), CONTINI (1976), COX & GALLOIS (1981), and HANTZPERGUE & LAFAURIE (1983). 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. HANTZPGERGUE (1987, 1989) 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 HANTZPERGUE 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).

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 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 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

Type species: *Ammonites gravesianus* D'ORBIGNY, 1847.

Included species: *Ammonites gigas* ZIETEN, 1830; *Ammonites gravesianus* D'ORBIGNY, 1847; *Ammonites irius* D'ORBIGNY, 1847; *Gravesia lafauriana* HANTZPERGUE, 1987 (for synonyms see HANTZPERGUE 1989).

Gravesia gravesiana (D'ORBIGNY) [M] Fig. 3

* 1847 *Ammonites Gravesianus* D'ORBIGNY, p. 559, pl. 219, figs. 1-2.
non 1915 *Holcostephanus* (*Gravesia*, SALFELD) *Gravesianus* D'ORB. – SCHNEID, S. 166, pl. 7, fig. 1. [= *G. gigas*]
1959 *Gravesia gravesiana* (D'ORBIGNY). – BARTHEL, p. 47, pl. 5, figs. 1-6.
1959 *Gravesia gravesiana* (D'ORBIGNY). – BERCKHEMER & HÖLDER, p. 62, fig. 35c.
1963 *Gravesia gravesiana* (D'ORBIGNY). – HAHN, p. 99, pl. 10, figs. 3-4, pl. 13, fig. 2 only.
1963 *Gravesia polypleura* n. sp. – HAHN, p. 101, pl. 11, fig. 1 only.
non 1974 *Gravesia* sp. – ZAKHAROV & MESEZHNIKOV, p. 177, pl. 1, fig. 2.
1980 *Gravesia gravesiana* (D'ORBIGNY). – OHMERT & ZEISS, p. 9.
1987 *Gravesia gravesiana* (D'ORBIGNY). – HANTZPERGUE, p. 247, pl. 19, figs. a-c.
1989 *Gravesia gravesiana* (D'ORBIGNY). – HANTZPERGUE, p. 205, pl. 19, figs. a-c. [with list of further synonyms]
1993a *Gravesia gravesiana* (D'ORBIGNY). – SCHWEIGERT, p. 173, non p. 172.
1994 *Gravesia gravesiana* (D'ORBIGNY). – ZEISS, p. 517.
1995 *Gravesia gravesiana* (D'ORBIGNY). – SCHWEIGERT & SCHERZINGER, p. 314, fig. 2b.
1996 *Gravesia gigas intermedia* HANTZPERGUE. – ZEISS et al., p. 134.
1996 *Gravesia gravesiana* (D'ORBIGNY). – ZEISS et al., p. 134.
1996a *Gravesia gravesiana* (D'ORBIGNY) [M]. – SCHWEIGERT, p. 298.
1997 *Gravesia gigas intermedia* HANTZPERGUE. – DIMKE & ZEISS, p. 77ff., pl. 11, fig. 1.
1997 *Gravesia gravesiana* (D'ORBIGNY). – DIMKE & ZEISS, p. 77ff., pl. 11, fig. 2, pl. 12, fig. 2.
1999 *Gravesia 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. *Gravesia 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 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 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 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] Fig. 4

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, *laisackerensis* 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 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* HANTZPERGE 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 tolverense* 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).

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 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): *Euvirgalithacoceras* ZEISS, SCHWEIGERT & SCHERZINGER, *Lithacoceras* HYATT s.l., *Hegovisphinctes* ZEISS, SCHWEI-

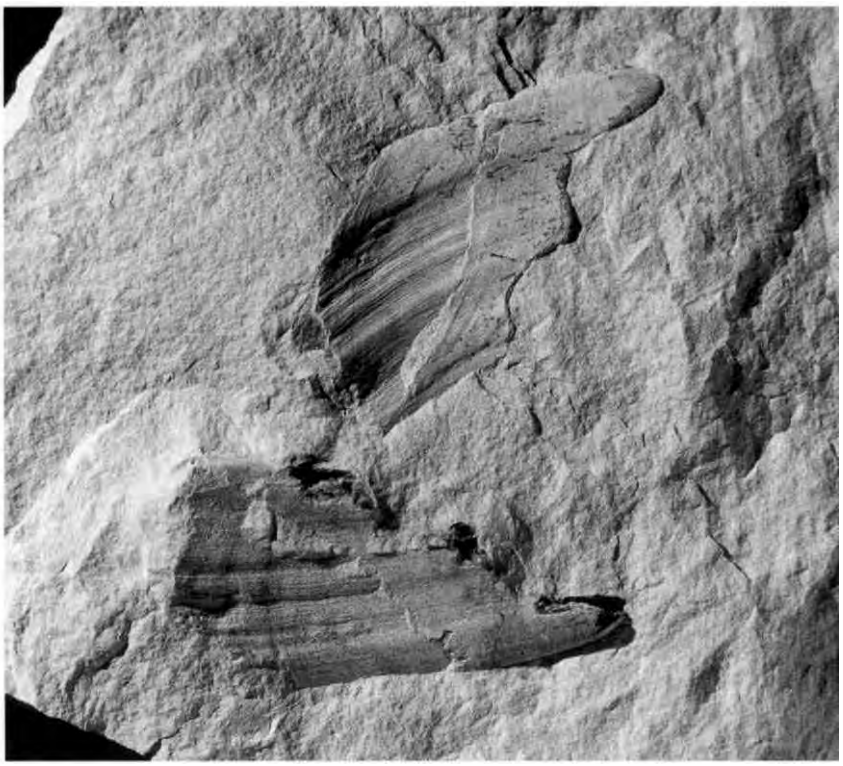


Fig. 5. Fragment of an aptychus probably belonging to *Gravesia gravesiana* (D'ORBIGNY), Lower Tithonian, Hangende Bankkalke Formation, KWV Jura-Steinwerke Liptingen; Hybonotum Zone, *laisackerensis* Horizon (SMNS 66206, leg. H. PARENT). – Width of photograph 165 mm.

GERT & SCHERZINGER, and *Hoelderia* OHMERT & ZEISS. They are all unequivocal perisphinctids which differ from *Gravesia* by their high-oval, not coronate whorl sections. In Upper Jurassic perisphinctids 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

Fig. 6. Detail of aptychus 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 punctation 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 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 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 1996b; HANTZPERGUE et al. 1998a, b; SCHERZINGER & MITTA, 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 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-

GUE still exhibits a rather evolute coiling and a coarse biplicate ribbing of the juvenile whorls. In *Tolvericeras*, however, a typical perisphinctid lappet is developed in the microconchs thus contrasting the herein recorded sinuous peristomal 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 perisphinctid 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 & MESEZHNIKOV 1974; MESEZHNIKOV 1984) are highly questionable and more likely represent homoeomorphic perisphinctoids, especially in respect of their different suture lines, with a very characteristic umbilical lobe U_1. *Gravesia* (?) *triplicata* MESZHNIKOV, 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* MESEZHNIKOV, 1974 (see ZAKHAROV & MESEZHNIKOV 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*' *loupekinei* published by VERMA & WESTERMANN (1984) from the Kimmeridgian/Tithonian boundary beds of Kenya represent an offshoot of katroliceratids 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 katroliceratids, 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 *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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Addresses of the authors:

Dipl.-Ing. (FH) ARMIN SCHERZINGER, Hewenstraße 9, 78194 Immendingen-Hattingen, Germany;
e-mail: Armin.Scherzinger@t-online.de
Dr. GÜNTER SCHWEIGERT, Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany;
e-mail: schweigert.smns@naturkundemuseum-bw.de
Dr. HORACIO PARENT, Laboratorio de Paleontología, Universidad Nacional de Rosario, Pellegrini 250, 2000 Rosario, Argentina;
e-mail: parent@fceia.unr.edu.ar