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Allometric growth and intraspecific variability in the basal Carboniferous ammonoid *Gattendorfia crassa* SCHMIDT, 1924

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with 7 figures

Abstract: *Gattendorfia crassa* is an Early Carboniferous (Mississippian) goniatite species with strikingly allometric conch growth. Analysis of 15 high-precision cross-sections of this species demonstrates the small intraspecific variability of some of the conch form characters, but remarkable variability in others. While the whorl expansion rate, umbilical width, and conch thickness vary within narrow limits, the expansion rates of the whorl height and whorl width are remarkably plastic. Variability of most of the characters tends to be smallest in intermediate growth stages, whereas juveniles and adults are more variable. The differences in morphological plasticity are interpreted in terms of the function of the ammonoid conch, especially the orientation of the aperture during life.

Keywords: Ammonoidea, Early Carboniferous, Mississippian, ontogeny, allometry, intraspecific variability

Kurzfassung: *Gattendorfia crassa* ist eine unterkarbonische Goniatiten-Art mit auffallend allometrischem Gehäuse-Wachstum. Die Analyse von 15 Hochpräzisions-Querschnitten dieser Art zeigt die geringe intraspezifische Variabilität einiger Gehäuseparameter und die bemerkenswerte Variabilität in anderen Merkmalen. Während die Windungsexpansionsrate, Nabelweite und Gehäusebreite nur in engen Grenzen variieren, sind die Expansionsraten der Windungshöhe und Windungsbreite sehr plastisch. Bei den meisten Merkmalen ist die Variabilität in intermediären Stadien am geringsten, während Jugend- und Adultstadien sehr variabel sind. Die Unterschiede in der morphologischen Plastizität werden durch die Funktion des Gehäuses interpretiert, besonders durch dessen Orientierung der Mündung zu Lebzeiten.

Schlüsselwörter: Ammonoidea, Unterkarbon, Mississippium, Ontogenie, Allometrie, Variabilität

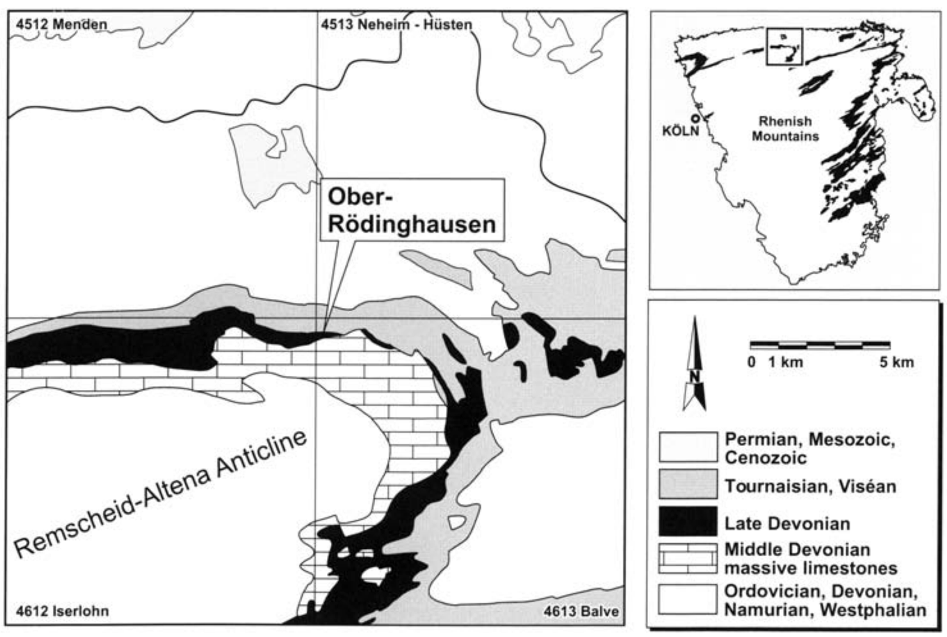

Fig. 1. Location of the Ober-Rödinghausen railway cutting at the northern margin of the Rhenish Mountains of Germany.

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Introduction

Post-event intervals are sometimes characterised by innovative phases with rapid adaptive radiations of organisms. Such an evolutionary pattern seems to be evident in the earliest Carboniferous ammonoids. After the almost complete extinction of the class Ammonoidea during the Hangenberg Event, when nearly all the clymeniids and most of the goniatite lineages disappeared, only the prionoceratid ammonoids flourished in the earliest Carboniferous, but were very diverse (VÖHRINGER 1960; RUAN 1981; KORN 2000).

Ammonoids from this time interval are known from two regions in particular:

- Rhenish Mountains, Germany (especially from the railway cutting near Ober-Rödinghausen; SCHMIDT 1924; VÖHRINGER 1960), and
- Guizhou, China (especially from Wangyou; SUN & SHEN 1965; RUAN 1981).

In the railway cutting section at Ober-Rödinghausen (Fig. 1), VÖHRINGER (1960) recognised approximately 45 different species, which he collected from 10 successive beds (Fig. 2). Therefore, stratigraphic control for this occurrence is good. The assemblage from Wangyou shows the same diversity (45 species), but was not collected bed-by-bed, thus stratigraphic assignment is rather limited for this assemblage.

Basal Carboniferous ammonoids show a wide range of conch morphologies and occupy a wide range of morphospace. Completely involute, discoidal to globose conchs, and also serpenticonic geometries with a full range of intermediates (e.g. with open umbilicate inner whorls and more involute adults) can be recognised. They demonstrate gradual evolution of this group.

The analysis of cross-sections seems to be the most promising method for uncovering phylogenetic relationships between the species of these ammonoids and was first attempted by VÖHRINGER (1960). In this monograph, almost all the species were documented by an illustration of the cross-section. Intraspecific variability was not investigated at that time, but forms one of the topics of the present paper. For this purpose, a large number of specimens were sectioned and serve as the basis for the following account.

Gattendorfia crassa is one of the most spectacular ammonoids from the basal Carboniferous "*Gattendorfia* Stufe", because it displays extremely allometric growth with several successively different conch shapes (Figs. 3, 4). Juveniles are serpenticonic, whereas adults are pachyconic with a small umbilicus (VÖHRINGER 1960). This species, which occurs rather commonly in the upper part of the Hangenberg Limestone of the Rhenish Mountains, is thus highly suitable for the biometric case study presented here.

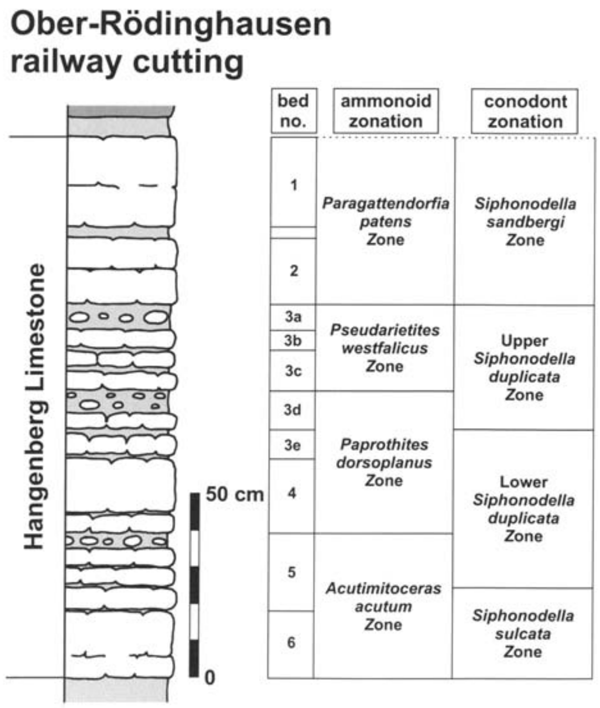

Fig. 2. Columnar sections of the Hangenberg Limestone in the Ober-Rödinghausen railway cutting; bed numbering and ammonoid stratigraphy after VÖHRINGER (1960).

Material and methods

A suite of 15 sectioned specimens of *Gattendorfia crassa* SCHMIDT, 1924 was used to investigate allometric growth and intraspecific variability. The specimens range, in their maximal sizes, from 14 to 52 millimetres, and eight of them display the early juvenile ontogeny. The entire material comes from bed 2 (*Paragattendorfia patens* Zone) of the Hangenberg Limestone, exposed in the railway cutting near Ober-Rödinghausen (Rhenish Mountains; Fig. 1), and was collected by E.V. during the 1950s. The prepared cross-sections were ground and polished by E.V., and further processing, including drawing of the sections and measurement of the conch dimensions, was carried out by D.K.

The polished sections were scanned in high resolution mode (2400 dpi), and acetate peels were produced for additional scanning. These scans were used as templates for the drawing of the whorls (Fig. 4) using Corel Draw©, and for obtaining the exact dimensions of the conchs. These were used to calculate the whorl ratios and growth rates of the various conch parameters.

The computer images of the cross sections yielded three of the basic conch parameters for each half volution (Fig. 5):

- conch diameter (dm)
- whorl width (ww)
- whorl height (wh)

Using these basic parameters, additional secondary conch parameters were computed:

- umbilical width (uw) = dm_1-wh_1-wh_2
- apertural height (ah) = dm_1-dm_2
- imprint zone (iz) = wh_1-ah or wh_1-(dm_1-dm_2)

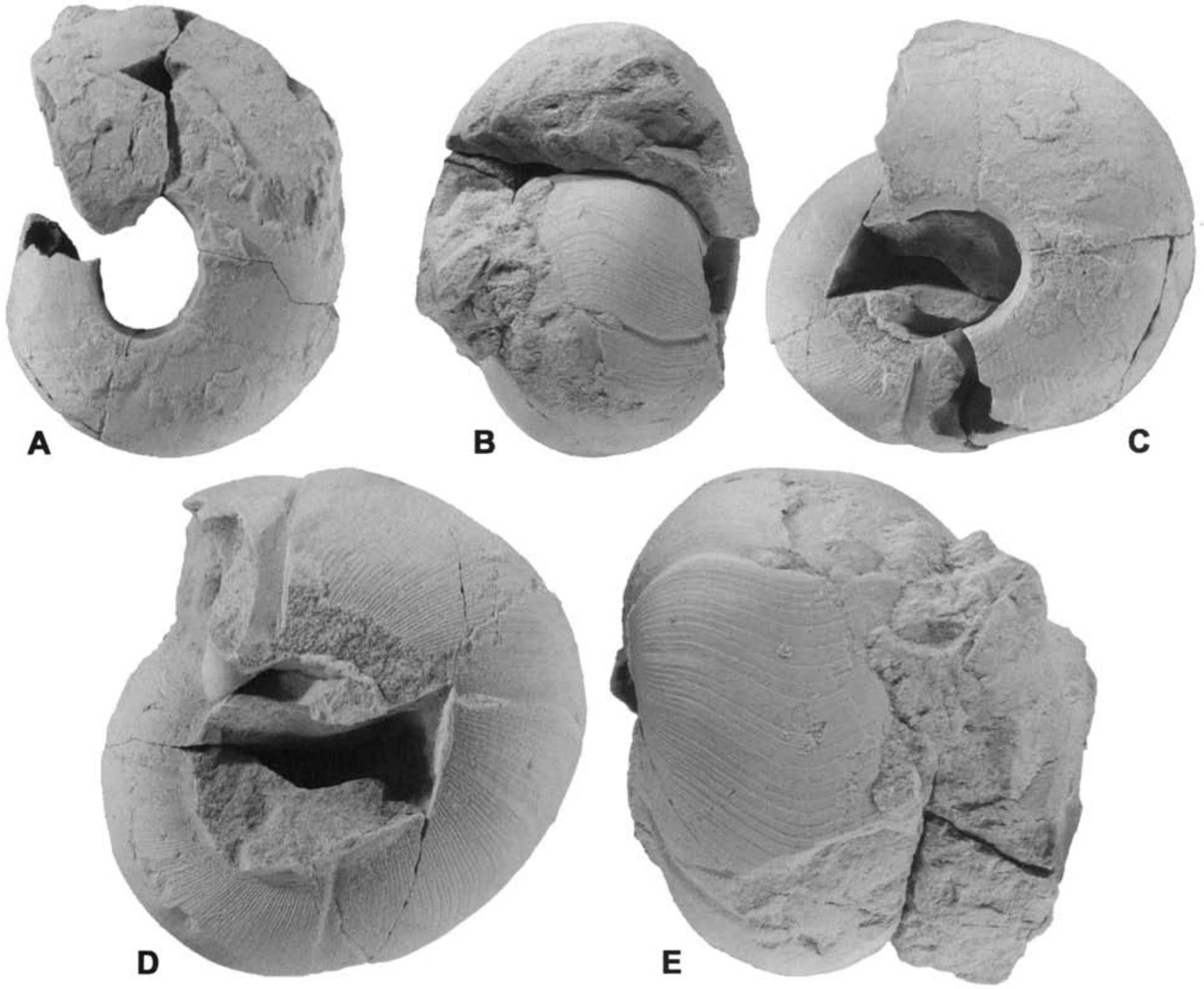

Fig. 3. Holotype (BGRB X5714) of *Gattendorfia crassa* SCHMIDT, 1924 from the Ober-Rödinghausen railway cutting (coll. SCHMIDT 1920). – **A**: Part of the outer whorl, ×1. **B**, **C**: Part of the last whorl removed, ×1.25. **D**, **E**: Inner whorls, ×2.

Ratios and growth rates (expansion rates) were calculated in the following way:

- whorl expansion rate (WER) = $(dm_1/dm_2)^2$ or $[dm_1/(dm_1\text{-}ah)]^2$
- whorl height expansion rate (WHER) = $(wh_1/wh_2)^2$
- whorl width expansion rate (WWER) = $(ww_1/ww_2)^2$
- surface expansion rate (SER) = css_1/css_2
- conch cross section index (CCSI) = ww_1/dm_1
- whorl cross section index (WCSI) = ww_1/wh_1
- umbilical width index (UWI) = uw/dm_1 or $(dm_1\text{-}wh_1\text{-}wh_2)/dm_1$
- imprint zone rate (IZR) = $wh_1\text{-}ah/wh_1$ or $(wh_1\text{-}(dm_1\text{-}dm_2))/wh_1$

The calculated conch ratios and growth rates were plotted in bivariate diagrams (Fig. 6) and were also statistically analysed. For this purpose, the total sum of 180 measurements was subdivided into sets of 15. The median value as well as the range of the middle two quartiles was computed for the 12 resulting groups and plotted in box-and-whiskers diagrams to illustrate ontogenetic fluctuations of variability (Fig. 7).

Repository: The examined material is housed in the Museum für Naturkunde, Berlin, catalogue numbers MB.C.5346 to MB.C.5358, in the Institut für Geowissenschaften, Tübingen, catalogue numbers GPIT 1130/100 and GPIT 1130/177, and in the Bundesanstalt für Geowissenschaften und Rohstoffe, Dienstbereich Berlin, catalogue number BGRB X5714.

Conch form analyses

Four different conch growth rates (WER, WHER, WWER, and SER) and the conch ratios (CCSI, WCSI, UWI, and IZR) were studied in detail. The plots for each of these conch parameters (Fig. 6) show a number of characteristics revealing the fundamental effects of allometric growth of the conch and its intraspecific variability in *Gattendorfia crassa*:

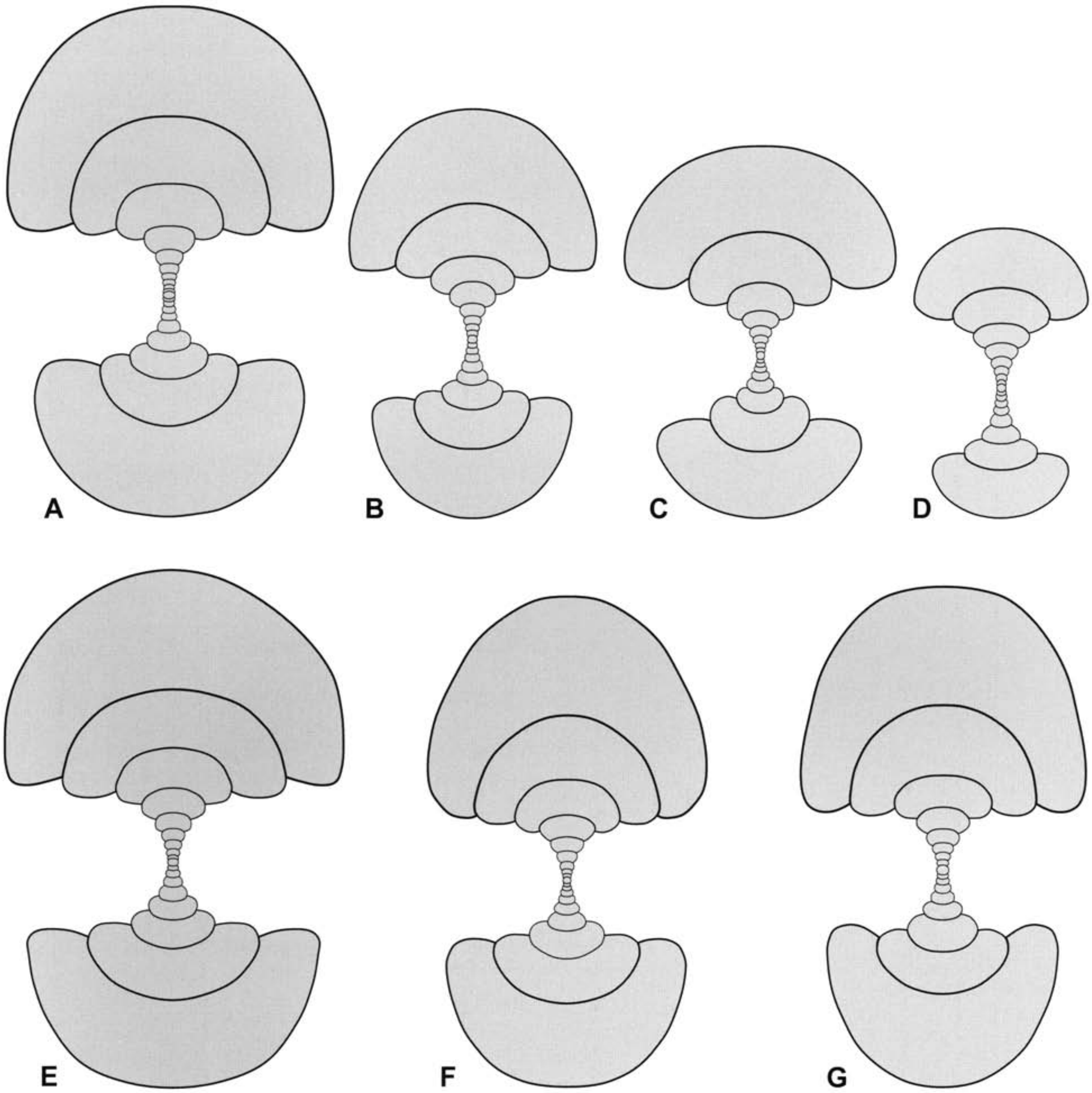

Fig. 4. Selected cross sections of *Gattendorfia crassa* SCHMIDT, 1924 from bed 2 of the Ober-Rödinghausen railway cutting (coll. VÖHRINGER), all ×2. – **A**: GPIT 1130/100. **B**: GPIT 1130/177. **C**: MB.C.5354. **D**: MB.C.5355. **E**: MB.C.5346. **F**: MB.C.5352. **G**: MB.C.5353.

- During ontogenetic development, the whorl expansion rate (WER) shows only minor fluctuations (Fig. 6A). The WER reaches highest values (median value 1.7–1.8) in the initial stage (conch diameter up to 2 mm). During early ontogeny, this value decreases to less than 1.5 in the stages between 5 and 8 mm diameter, and, at maturity, it increases again reaching a value of 1.75 at 40 mm conch diameter.

  Intraspecific variability is relatively low at all growth stages. There is a trend toward slightly less variability (Fig. 7A) in the intermediate stages between conch diameters of 4 and 16 mm, but the differences between growth stages are inconspicuous.

- The expansion rate of whorl height (WHER) increases continuously during ontogeny (Fig. 6B), but there is a more rapid heightening of the whorls at stages larger than 7 mm diameter. The WHER plot shows two different trends in adults, but it is not certain if this reflects two clearly definable morphogroups.

  An interesting feature of the WHER is that preadults of 20–30 mm conch diameter have a much wider range of variability than juveniles up to 9 mm conch diameter. Variability is thus highest when the WHER maximum is reached (Fig. 7B).

- By contrast to the WHER, the expansion rate of the whorl width (WWER) does not show a continuous in-

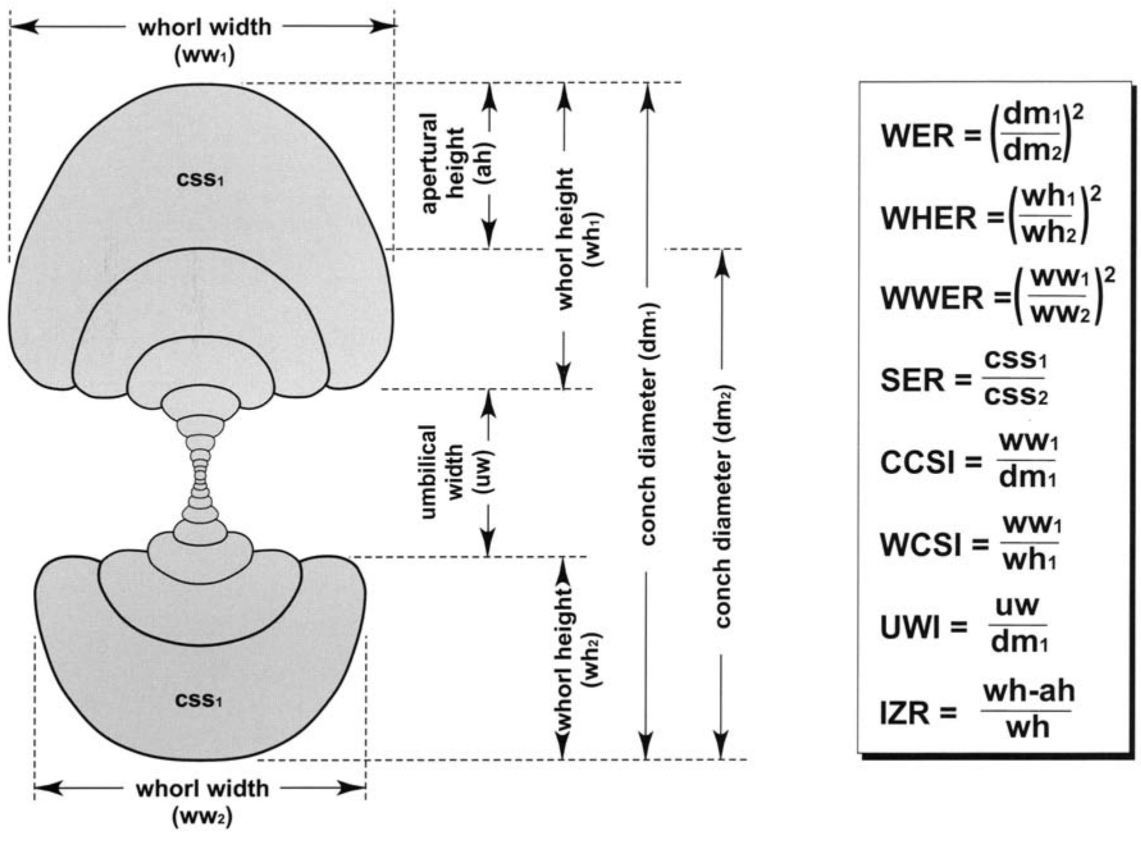

Fig. 5. Conch parameters and ratios as used in the text.

crease (Fig. 6C). A maximum of relative whorl widening (median value 1.9, middle two quartiles range from 1.7 to 2.2) is at conch diameters between 7 and 12 mm. After this, there is a slight but continuous decrease toward maturity.

By contrast to the other characters discussed above, variability is most prominent in the intermediate stage, i.e., around 10 mm diameter, corresponding to the point when the maximum WWER is reached (Fig. 7C). Juveniles show remarkably little variation, and adult conchs also tend to have a more stable WWER.

- The WCSI plot clearly exhibits ontogenetic changes in whorl cross section shape. After a slight initial increase of the WCSI, a minimum value (1.65) is reached at conch diameters of 2.5 mm. Between 2.5 and 10 mm diameter, a continuous increase towards a median value of 2.0 is observed, the, at stages larger than 15 mm, there is a pronounced decrease of the WCSI to approximately 1.2 at 40 mm diameter (Fig. 6D).

  Intraspecific variability is not particularly high at any growth stage (Fig. 7D). As is evident for the UWI, the intermediate stages, i.e., between 7 and 20 mm conch diameter, are less variable than for early juveniles and adults.
- The umbilical width index (UWI) experiences dramatic ontogenetic changes that are clearly visible in the illustrations of the cross-sections (Fig. 4). At the initial stage, the umbilicus has a width of 1/3 of the conch diameter. Up to approximately 3.5 mm in diameter, a continuous increase in the UWI is observed, and between 3.5 and 9 mm diameter, the median value of the UWI is greater than 0.6. Stages larger than 9 mm then show then a relatively steady decrease of the UWI, so that at 40 mm diameter, the umbilicus has a width of only 1/5 of the conch diameter (Fig. 6E).

  This value shows only minor intraspecific variability (Fig. 7E), and again variability is lowest in the intermediate stage between conch diameters of 3 and 15 mm.
- The plot for the imprint zone rate (IZR) runs largely counter to the UWI plot because the closure of the umbilicus automatically leads to a wider embracement of the previous whorls. In the juvenile serpenticonic stage, the whorls show only a small degree of embracement, with an IZR of approximately 0.17 between conch diameters of 3 and 8 mm. Later in ontogeny, a continuous increase in this value reaching 0.50 at 40 mm dm is observed (Fig. 6F).

  Intraspecific variability is most clearly recognisable in juveniles up to 8 mm diameter (Fig. 7F).

Discussion

Gattendorfia crassa can be regarded as a species that exhibits low intraspecific variability, evident from its ho-

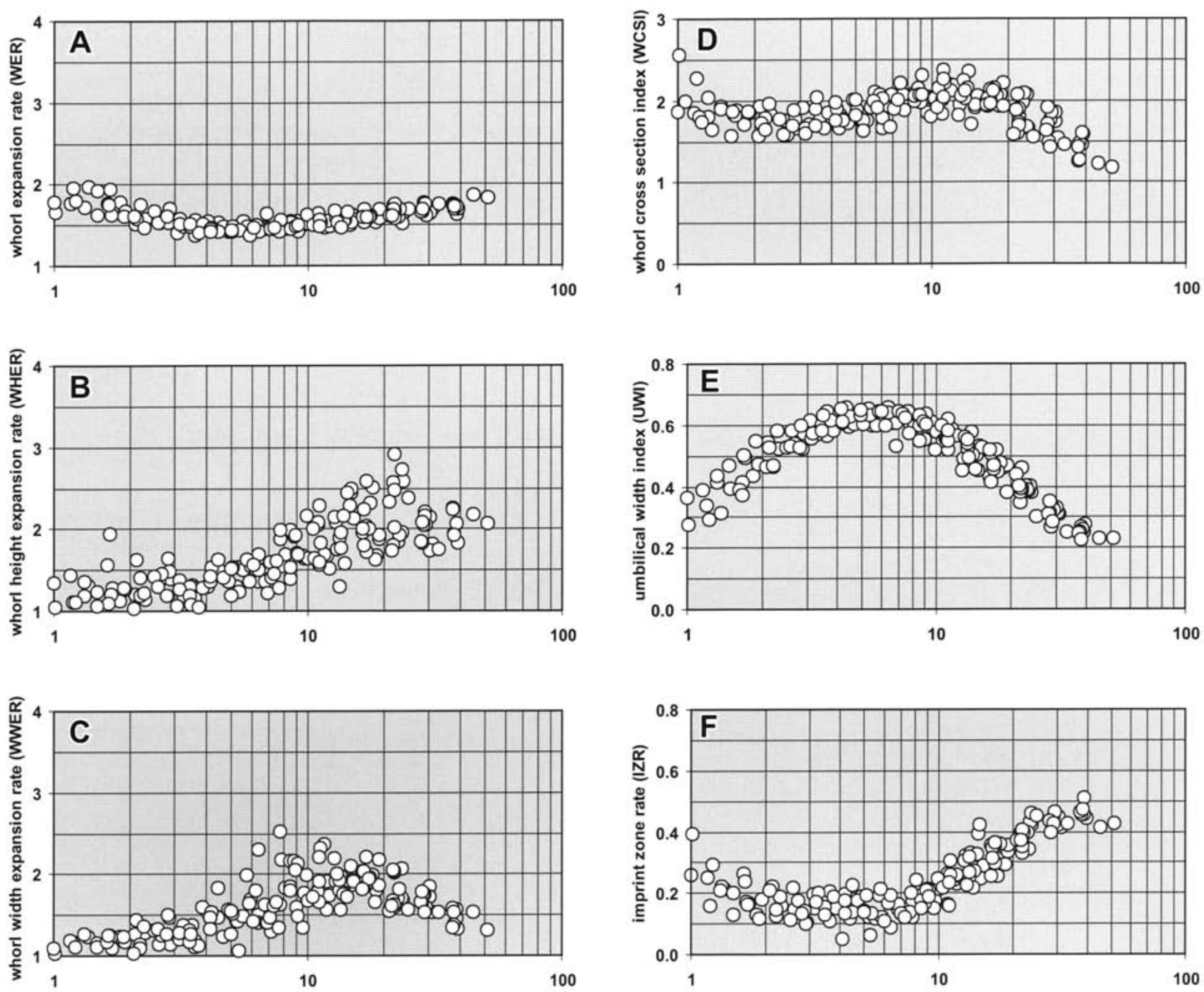

Fig. 6. Bivariate diagrams showing the ontogenetic development of the major conch ratios and expansion rates of *Gattendorfia crassa* SCHMIDT, 1924 from bed 2 of the Ober-Rödinghausen railway cutting.

mogenous distribution in morphospace. An interesting feature is the remarkably different degree of variability of the conch parameters analysed. This is especially expressed in the differences between the WER, WHER, and WWER plots. Of these, only the WER can be regarded as a stable character. The reason for the stability of the WER can be found in functional constraints; the WER largely controls the length of the body chamber and hence the orientation of the aperture of the living animal (SAUNDERS & SHAPIRO 1986; OKAMOTO 1996). Such constraints can not be postulated for the WHER, and probably not for the WWER.

Ontogenetic development of the whorl height and whorl width controls the size of the umbilicus and the general conch shape; both are responsible for hydrodynamic properties of the conch. These constraints are obviously less strict than those on the orientation of the aperture, an interpretation that is supported by the observation that the WER is stable in many ammonoid groups, e.g. within the genus *Acutimitoceras*, a close relative to *Gattendorfia*, where it ranges from 1.8 to 2.0. By contrast to this, species of *Acutimitoceras* show very different conch shapes, ranging from discus-shaped to globose (VÖHRINGER 1960; KORN 2000).

There is no obvious explanation for the ontogenetic fluctuations of intraspecific variability. The high juvenile variability seen in the WER and UWI may be an artifact, because any slight imprecision in the grinding of the specimens may result in more prominent errors in juveniles. At the same time, the WHER and WWER plots show little early juvenile plasticity, which speaks for the accuracy of the preparations. A striking feature is the degree of adult variability which, in almost all of the conch parameters investigated, is considerably higher than in intermediate growth stages.

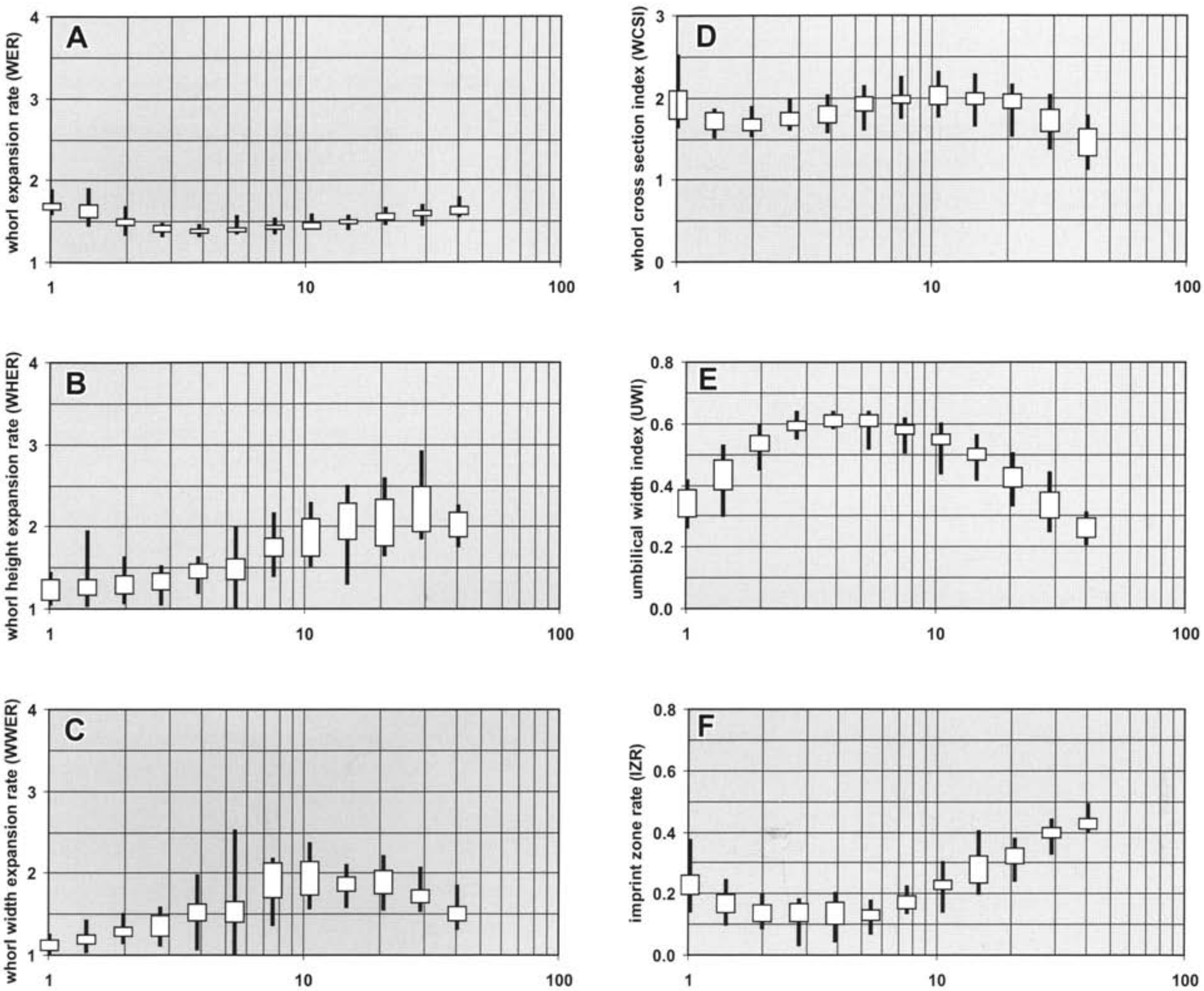

Fig. 7. Box-and-whiskers diagrams showing the ontogenetic variations of intraspecific variability of the major conch ratios and expansion rates of *Gattendorfia crassa* SCHMIDT, 1924 from bed 2 of the Ober-Rödinghausen railway cutting. Each box is calculated by a set of 15 data, bold line refers to the total range, boxes refer to the extension of the middle two quartiles.

Results

The following results were obtained from the biometric analysis:

- General conch ontogeny
  - *Gattendorfia crassa* displays a markedly allometric growth pattern
  - The conch has three principal morphological stages
    - a serpenticonic early juvenile stage
    - a cadyconic intermediate stage
    - a pachyconic adult stage
- Development of conch characters
  - The WER shows little modification during ontogeny; it reaches a maximum of 1.7 (median value) at 1 mm diameter, a minimum of 1.4 at 4 mm, and a second maximum of 1.6 at 40 mm.
  - The WHER is lowest in early ontogeny with a median value of 1.2 at a conch diameter of 1 mm. There is a slight increase up to a value of 1.5 at diameter of 5 mm, and an accelerated increase up to 2.25 at 30 mm. In the adult stage, a decrease to a value of 2.0 is observed.
  - The WWER shows a relatively low value of 1.2 at 1 mm diameter and increases steadily to a maximum of 1.9 at 10 mm. At the adult stage, a decrease to a value of 1.5 is observed.
  - The WCSI has a low value (1.7) at 2 mm diameter and reaches a maximum of 2.0 at 10–15 mm, decreasing to 1.5 in adult examples with a conch diameter of 40 mm.
  - The UWI has a value of 0.35 at 1 mm diameter, reaches a maximum of little more than 0.60 at 4 mm, and decreases toward a minimum of 0.25 at a conch diameter at 40 mm.
  - The IZR exhibits an almost perfectly diametric pattern to that shown by the UWI.

- Intraspecific variability of conch characters
  - The WER shows little variability, and the intermediate stage tends to be less variable than juveniles and adults.
  - The WHER is much more variable than the WER; the maximal variability is seen in the adult stage, whereas juveniles and intermediates show less plasticity.
  - The WWER also shows high variability, but the intermediate stage is most variable.
  - The WCSI is also not very variable, and there is no clear pattern in the degree of variability during ontogeny.
  - The UWI shows little variability; intermediate stages tend to be less variable than juveniles and adults.

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